Universidade de Aveiro Departamento de Biologia
2012

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Gorgónias do Sul de Portugal: biologia, ecologia e conservação

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Tese apresentada à Universidade de Aveiro para cumprimento dos requesitos necessários à obtenção do grau de Doutor em Biologia, realizada sob a orientaccão científica da Professora Doutora Maria Marina Pais Ribeiro da Cunha, Professora Auxiliar do Departamento de Biologia da Universidade de Aveiro e do Doutor Luís Miguel Pinto Charneca Neves dos Santos, Investigador Auxiliar do Instituto Português do Mar e da Atmosfera.

João Cúrdia was supported by a PhD grant (SFRH/BD/29491/2006) from Fundação para a Ciência e a Tecnologia, co-funded by POPH/FSE.

to Susana and Martim

"We are tied to the ocean. And when we go back to the sea, whether it is to sail or to watch - we are going back from whence we came."

— John Fitzgerald Kennedy

"By three methods we may learn wisdom: First, by reflection, which is noblest; Second, by imitation, which is easiest; and third by experience, which is the bitterest."

— Confucius

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agradecimentos /
acknowledgements

Ending a work like this is the culmination of a long “journey”. However, its results would be undoubtedly different without the collaboration of several people and entities, which help and support is materialized throughout this thesis.

First of all I would like to acknowledge the director of IPIMAR, for accepting the development of this study in the facilities of this Institute. It would be virtually impossible to do all the fieldwork without the logistic support of the institution, namely concerning diving. Even though displaced from Universidade de Aveiro, the university provided the necessary infrastructures at every solicitation and the staff of all the services that I used were always extremely helpful and dedicated to solve all sorts of problems. I am also extremely grateful to FCT - Fundação para a Ciência e Tecnologia - for funding a scholarship during a four-year period (SFRH/BD/29491/2006).

My supervisors, Dr. Marina Cunha (University of Aveiro) and Dr. Miguel Neves dos Santos (INRB, I.P./IPIMAR) supported and guided me during this entire “journey” and were always available for bureaucratic and scientific demands. Their contributions were invaluable at all phases of the thesis, directing me towards the objectives of my research and focusing my efforts as needed. Furthermore, they were complementary, providing me a wide array of knowledge and experience that I tried to acquire, and, when needed, motivated me to contact people that could help with my questions. To both of you, thank you for the friendship and endless support during the last years.

I am extremely grateful to Dr. Pablo Gonzalez from Universidad de Sevilla, who helped me on the study of the reproductive cycle of gorgonians and patiently answered all sorts of questions regarding cnidarians. His devotion to science is such that every time I visited him at Sevilla, I wanted to do new things and spend more time in the lab trying to solve new problems and elaborate new hypothesis.

To Jorge Gonçalves, Pedro Monteiro and Carlos Afonso for sharing their data, for the opportunity to conduct studies that were not programmed initially but most of all for their enthusiasm in discussing our underwater observations, which definitely contributed for a more exact and solid understanding of the patterns, diversity and processes that structure and govern the benthic communities in rocky areas of the Algarve.

I am also grateful to Dr. Miguel Gaspar, for sharing his knowledge on various fishing effects on the benthic communities of the Algarve, but more important, for helping me, for motivating me and share my interest on the subjects that I worked on. His contagious joy was also extremely important to counter-balance set backs.

To Pedro Lino, my main dive buddy but also Marco Cerqueira and Sérgio Amorim for diving and helping in the underwater fieldwork. Special thanks are due to Pedro Lino as my main advisor in underwater techniques, computer related things and brainstorming on my research issues. Thanks also for all the rides home that provided me the extra time needed to finalize many tasks.

To my colleagues from the laboratory of benthos in IPIMAR, Rita Constantino, Fábio Pereira, Marco Cerqueira, Ana Moura and Marisa Barata for their friendship and help on the laboratory, especially for the real partnership atmosphere. To Paulo Vasconcelos for his friendship, the numerous advices on analysis and scientific writing but also for revising drafts of parts of this thesis. Special thanks are due to Marco Cerqueira, because he was a real globe trotter, helping me during dives, logistics and maintenance work and those other things that I now cannot remember...
To Jorge Ramos for the help on understanding some of the socio-economical aspects related to the sea. To Alexandre Pereira and Cláudia Roque for their friendship, interest and, jointly with Jorge Ramos, numerous and diversified talks during lunch breaks. To Paula Moura for the help during histological procedures and enormous patience to discuss and remind me the techniques.
To the technicians José Luís Sofia and Tibério Simões who were always available for helping me during sampling campaigns and all kinds of logistic nightmares. Their experience saved me many headaches and set backs.
To all the other colleagues of IPIMAR, thank you for your friendship.
To all the developers and maintainers of the open source software, especially LaTeXand R and their libraries and packages. Thanks also for all the altruistic people that post the answers to questions that arise while using these scientific helpers.
To my friends from Aveiro and Coimbra: Ana Ré, Ascensão Ravara, Andrea Baptista, Nuno Branco, Hermínia Castro, Leandro Sampaio, Margarida Clemente, Maria João Almeida and Susana Silva, although spatially distant were always supportive and present. Thank you for your friendship!
To my closest family, but especially to my parents that always supported me, giving me the confidence to proceed, to adventure myself but assuring that my safe port is present and always near... I continue to be completely overwhelmed by your endless love!

To my wife Susana, thanks for everything! Without your support I would never have concluded this adventure. You were always supportive... your many complaints were but a few, considering what you had to put up with... and they were fair! Especially in the final part of the thesis, you showed incredible stamina and capacity, but most of all, sympathy and real partnership, reviewing, discussing and helping in whatever I needed. You were my stronghold and the very first to always help me when I needed most. Thank you for everything!

Finally to my beloved son Martim. Thank you Martim for being the greatest joy of my life! I am sorry for every time that I could not play football or build a Lego with you because I was working. I hope that you can forgive me on that! You are the best son that a man can dream of and every time you surprise me, or annoy me or make me laugh, is a moment that I have lived fully, that boosts me to excel myself. You fulfil my heart with endless love and I cannot resist to your charms... You make my day, every day!

palavras-chave / **keywords**

gorgónias; *Leptogorgia*; *Eunicella*; fauna epibentónica associada; reprodução; pressão antropogénica; pesca; mergulho; Algarve

resumo / **summary**

O papel ecológico das gorgónias (Octocorallia: Alcyonacea) nos fundos marinhos rochosos é mundialmente reconhecido. Contudo, a informação acerca da ecologia e biologia das espécies de gorgónias nas zonas temperadas do NE Atlântico é manifestamente escassa, especialmente tendo em consideração as actuais perturbações globais, regionais e locais. Nos fundos rochosos da costa algarvia até aos 30 m, verificou-se que várias espécies de gorgónias são abundantes e frequentes, nomeadamente *Eunicella labiata*, *Eunicella gazella*, *Eunicella verrucosa*, *Leptogorgia lusitanica* e *Leptogorgia sarmentosa*. As populações de gorgónias são co-dominadas por diferentes espécies que apresentaram elevados índices de associação, indicando reduzidos níveis de competição entre elas. Em todo o caso, a estrutura dos povoamentos diferiu com as condições locais. Todas as espécies evidenciaram padrões de distribuição semelhantes ao longo do gradiente de profundidade, i.e. a abundância aumenta significamente com a profundidade após os 15 m. A profundidades mais baixas (até aos 15 m), a distribuição das gorgónias parece ser condicionada por factores abióticos e pela competição com algas. Com efeito, os padrões de distribuição espacial das espécies de gorgónias na costa algarvia são determinados pela interacção de pressões naturais e antropogénicas (ex. pesca). Ainda que as colónias de maior tamanho não tenham sido restritas a áreas menos pescadas, em áreas mais perturbadas pela pesca, a distribuição dos tamanhos das colónias estava maioritariamente desviada para tamanhos mais pequenos. Os efeitos das perturbações naturais nas populações de gorgónias foram evidenciados pela ocorrência de padrões demográficos distintos em áreas vizinhas sujeitas a níveis semelhantes de pressões antropogénicas. Estes estudos demonstraram, ainda, que os efeitos na distribuição de frequências de tamanho das colónias são dependentes das espécies de gorgónias em causa: *Eunicella labiata* não parece ser afectada; *Leptogorgia sarmentosa* é tendencialmente afectada por pressões antropogénicas; *Eunicella gazella* e *Leptogorgia lusitanica* aparentam ser afectadas, quer por pressões naturais, quer por pressões antropogénicas. Os efeitos verificados nos padrões da distribuição de frequências de tamanho, particularmente a tendência para o desvio destas frequências para tamanhos mais pequenos em áreas sujeitas a perturbações, poderão ter consequências para a biodiversidade dos fundos sublitorais rochosos na costa algarvia.

Com efeito, o presente estudo apoia o paradigma geral de que os corais são habitats que suportam comunidades de elevada biodiversidade e abundância. Num dos poucos estudos que examinam a relação entre as gorgónias e as suas comunidades de invertebrados epibentónicos, foi verificado que as gorgónias (*Eunicella gazella* e *Leptogorgia lusitanica*) sustentam comunidades ricas (11 phyla, 181 taxa) e abundantes (7284 indivíduos). Estas comunidades são dominadas por anfípodes, mas os poliquetas tiveram um grande contributo para os níveis elevados de biodiversidade. Verificou-se, igualmente, que o tamanho da colónia desempenha um papel fundamental na biodiversidade, na medida em que as colónias de menor tamanho apresentaram um contributo mais baixo, comparativamente às médias e grandes. Ainda que ambas as gorgónias partilhem a maioria das espécies amostradas, 11 e 18 taxa foram exclusivos de *Eunicella gazella* e *Leptogorgia lusitanica*, respectivamente (excluindo indivíduos com presenças únicas). No entanto, a maioria destes taxa eram ou pouco abundantes ou pouco frequentes. A excepção foi a presença de planárias (Turbellaria) de coloração branca nas colónias de *Eunicella gazella*, provavelmente beneficiando do efeito de camuflagem proporcionado pelos ramos com a mesma coloração. Com efeito, a complementaridade entre as comunidades epibentónicas associadas a ambas as gorgónias diminuiu quando usados os dados de presença/ausência, sugerindo que os padrões de biodiversidade são mais afectados pelas alterações na abundância relativa das espécies dominantes do que pela composição faunística. As comunidades de epifauna bentónica associadas a estas gorgónias não só apresentaram valores elevados de α-diversidade, como de β-diversidade, resultantes de padrões intrincados de variabilidade na sua composição e estrutura. Ainda que o conjunto de espécies disponíveis para colonização seja, na generalidade, o mesmo para ambos os locais, cada colónia apresenta uma parte deste conjunto. Na sua totalidade, as colónias de gorgónias poderão funcionar como uma metacomunidade, mas a estrutura das comunidades associadas a cada colónia (ex. número total de espécies e abundância) parecem depender dos atributos da colónia, nomeadamente superfície disponível para colonização (altura, largura e área), complexidade e heterogeneidade (dimensão fractal e lacunaridade, respectivamente) e cobertura epibentónica "colonial" (ex. fauna colonial e algas macroscópicas; CEC). Numa primeira tentativa para quantificar a relação entre as gorgónias e os invertebrados epibentónicos a elas associados (em termos de abundância e riqueza específica), verificou-se que a natureza e a intensidade destas relações dependem da espécie hospedeira e variam para os grupos taxonómicos principais. No entanto, independentemente do grupo taxonómico, a riqueza específica e a abundância estão significativamente correlacionadas com a CEC. Com efeito, a CEC provavelmente devido a um efeito trófico (aumento da disponibilidade alimentar directo ou indirecto), combinado com a superfície disponível para colonização (efeito espécies-área) foram as variáveis mais relacionadas com os padrões de abundância e riqueza específica.

Por outro lado, ainda que a complexidade estrutural seja frequentemente indicada como um dos factores responsáveis pela elevada diversidade e abundância das comunidades bentónicas associadas a corais, a dimensão fractal e a lacunaridade apenas foram relevantes nas comunidades associadas a *Leptogorgia lusitanica*. A validade do paradigma que defende que a complexidade estrutural promove a biodiversidade poderá ser, então, dependente da escala a que se realizam os estudos. No caso das gorgónias, o efeito da complexidade ao nível dos agregados de gorgónias poderá ser muito mais relevante do que ao nível da colónia individual, reforçando a importância da sua conservação como um todo, por forma a preservar a diversidade de espécies hospedeiras, o seu tamanho e estrutura. Actividades antropogénicas como a pesca, podem, ainda, ter efeitos negativos ao nível da reprodução de espécies marinhas. Analogamente ao verificado para os padrões de distribuição espacial das populações de gorgónias na costa algarvia, a informação relativa à sua reprodução é igualmente escassa. Os estudos realizados em populações de *Eunicella gazella* a 16 m de profundidade, demonstraram que o desenvolvimento anual das estruturas reprodutivas é altamente sincronizado entre os sexos. A razão entre sexos na população foi de 1.09 (F:M), encontrando-se perto da paridade. A espermatogénese estende-se por 6 a 8 meses, enquanto que a oogénese é mais demorada, levando mais de um ano para que os oócitos se desenvolvam até estarem maduros. Antes da libertação dos gâmetas, foi observada uma elevada fecundidade nas fêmeas (27.30 ± 13.24 oócitos pólipo^{-1}) e nos machos (49.30 ± 31.14 sacos espermáticos pólipo^{-1}). Estes valores encontram-se entre os mais elevados reportados à data para zonas temperadas. A libertação dos gâmetas (não há evidência de desenvolvimento larvar, nem à superfície da colónia, nem no seu interior) occorre em Setembro/Outubro, após um período de elevada temperatura da água do mar. As fêmeas emitem oócitos maduros de elevadas dimensões, retendo, todavia, os oócitos imaturos que se desenvolvem apenas na época seguinte. Ainda que o efeito da pesca nas populações de gorgónias da costa do Algarve seja perceptível, às taxas actuais, o mergulho recreativo não aparenta afectar seriamente estas populações. Contudo, sendo uma indústria em expansão e conhecendo-se a preferência de mergulhadores por áreas rochosas naturais ricas em espécies bentónicas, futuramente poderá vir a afectar estes habitats. A monitorização de mergulhadores na costa algarvia mostrou que a sua maioria (88.6 %) apresenta comportamentos que podem impactar o habitat, com uma taxa média de contactos de 0.340 ± 0.028 contactos min^{-1}. Esta taxa foi mais elevada em mergulhadores com moderada experiência e na fase inicial do mergulho (0–10 min). Os contactos com as barbatanas e mãos foram comuns, resultando, maioritariamente, na resuspensão do sedimento, mas geralmente apresentando um impacto reduzido. Todavia, a fauna também foi afectada, quer por danos físicos, quer pela interacção com os mergulhadores, e num cenário de expansão significativa desta actividade, os impactos na fauna local poderão aumentar, com consequências para os ecossistemas de fundos rochosos da costa sul de Portugal. Na sua globalidade, a informação recolhida nos estudos que contemplam esta tese, por ser em grande parte totalmente nova para a região, espera-se que contribua para a gestão da zona costeira do Algarve.

keywords gorgonians; *Leptogorgia*; *Eunicella*; epibenthic associated fauna; reproduction; human pressure; fishing; scuba diving; Algarve

Abstract The ecological role of gorgonians (Octocorallia: Alcyonacea) in marine rocky bottoms is worldwide recognized, but the knowledge on the ecology and biology of NE Atlantic temperate species is insufficient, considering current global, regional and local threats. In the rocky bottoms of the Algarve several gorgonians were abundant and frequent down to 30 m, namely *Eunicella labiata*, *Eunicella gazella*, *Eunicella verrucosa*, *Leptogorgia lusitanica* and *Leptogorgia sarmentosa*. There is a high association of several gorgonian species that co-dominate assemblages, indicating low levels of competition among species. Nevertheless, gorgonian assemblages differed in structure, depending on local conditions. All species evidenced a similar depth pattern, i.e. abundance significantly increased with depth below 15 m. At shallower waters (up to 15 m), the distribution of gorgonians may be constrained by abiotic factors and competition with algae. Indeed, the spatial patterns of gorgonian populations along the southern coast of Portugal were driven by the interaction of both natural and anthropogenic pressures (namely fishing). Although larger colonies were not restricted to the sites with lower fishing pressure, gorgonian populations sampled in more intensively fished areas generally presented skewed distributions towards small sizes. The effects of natural disturbance events on the structure of gorgonian populations were evidenced by distinct demographic patterns in nearby areas under similar anthropogenic pressure. The present studies also showed that the effect of disturbance on size-frequency distribution of gorgonian populations is species-dependent: *Eunicella labiata* does not seem to be affected; *Leptogorgia sarmentosa* is likely affected mainly by anthropogenic pressures; *Eunicella gazella* and *Leptogorgia lusitanica* seem to be affected by both kinds of stress. The effects on size-frequency distributions patterns, namely the trend to skewed distribution towards small sizes under disturbance may have consequences for biodiversity of rocky sublittoral areas of the Algarve coast. Indeed, the present study supports the general paradigm that corals are habitats of enhanced abundance and biodiversity. In one of the few studies examining the relationship between gorgonians and their associated non-colonial epifaunal assemblages, gorgonians (*Eunicella gazella* and *Leptogorgia lusitanica*) were found to support rich (11 phyla, 181 taxa) and abundant (7284 individuals) assemblages. The present study supports the general paradigm that corals are habitats of enhanced abundance and biodiversity.

In one of the few studies examining the relationship between gorgonians and their associated non-colonial epifaunal assemblages, gorgonians (*Eunicella gazella* and *Leptogorgia lusitanica*) were found to support rich (11 phyla, 181 taxa) and abundant (7284 individuals) assemblages. These epifaunal assemblages were dominated by amphipods, but polychaetes had a relevant contribute to diversity. Colony size was found to have a relevant role on biodiversity patterns, with small size colonies contributing the least for overall biodiversity. Although both gorgonians shared most of the species collected, 11 and 18 taxa were exclusively associated with *Eunicella gazella* and *Leptogorgia lusitanica*, respectively (without considering singletons). Nevertheless, most of these exclusive taxa were either rare or uncommon. The exception was the presence of white flatworms Turbellaria in *Eunicella gazella* colonies probably taking advantage of crypsis with the white *Eunicella gazella* branches. Indeed, complementarity in the epifaunal assemblages associated with the two gorgonian hosts decreased when data was analysed after presence/absence transformation, suggesting that patterns of biodiversity are more affected by changes in the relative abundance of dominant species rather than in faunal composition. Gorgonian epifaunal assemblages not only showed high values of α-diversity but intricate patterns of variability in their composition and structure leading to high β-diversity. Although the total pool of species available in gorgonian colonies appears to be the same in both sites analysed, each colony yields a rather small set of this species pool. All together, the colonies may act as a metacommunity, but the structure of the assemblage in each colony (e.g. total number of species, dominance) apparently depends upon host attributes, namely the surface available for colonization (colony height, width and area), complexity and heterogeneity (fractal dimension and lacunarity respectively) and "colonial" epibiont cover (e.g. colonial fauna and macroscopic algae; CEC). In a first attempt to explicitly quantify the link between gorgonians and the abundance and species richness of associated non-colonial epifaunal invertebrates, the nature and intensity of these relationships were found to be not only host-dependent but varied from one taxonomic group to another. In all faunal groups associated with the two gorgonian hosts analysed, the species richness and abundance were strongly correlated with CEC. In fact, CEC possibly due to a trophic effect (direct or indirect enhancement of food availability) combined with the surface available for colonization (species-area effect) were the strongest predictors of species richness and abundance. On the other hand, although structural complexity is usually indicated as the main driver for the rich and abundant coral-associated assemblages, fractal dimension and lacunarity were only relevant for the assemblages associated with *Leptogorgia lusitanica*. The validity of the paradigm that structural complexity enhances biodiversity may be scale-dependent. In the case of gorgonians, the effect of complexity at the "garden" level may be much more relevant than at the individual colony level reinforcing the need for the conservation of gorgonian aggregation areas as a whole in order to preserve host diversity and size structure. On the other hand, although structural complexity is usually indicated as the main driver for the rich and abundant coral-associated assemblages, fractal dimension and lacunarity were only relevant for the assemblages associated with *Leptogorgia lusitanica*.

The validity of the paradigm that structural complexity enhances biodiversity may be scale-dependent. In the case of gorgonians, the effect of complexity at the "garden" level may be much more relevant than at the individual colony level reinforcing the need for the conservation of gorgonian aggregation areas as a whole in order to preserve host diversity and size structure. Anthropogenic activities like fishing may also have a negative impact on reproduction. Likewise the lack of information on distribution patterns of gorgonian assemblages and their role on local biodiversity patterns, no information was available for the Algarve coast concerning reproductive patterns of main gorgonian species. The annual development of reproductive structures in *Eunicella gazella* populations (16 m depth) was highly synchronized between sexes. The sex ratio of the population was 1.09 (F:M) being close to parity. The spermatogenic cycle extended for six to eight months, but the oogenic cycle was much longer, taking more than one year for mature oocytes to develop. Prior to spawning, high fecundity was observed in females (27.30 ± 13.24 oocytes polyp^{-1}) and males (49.30 ± 31.14 sperm sacs polyp^{-1}). These values are amongst the highest values reported to date in temperate gorgonians. Broadcast spawning of the gametes (no evidence of surface or internal brooding) occurred in September/October after a period of high sea surface temperatures during summer. Females release large sized mature oocytes but retain immature oocytes that develop only in the next season. Although the effect of fishing on gorgonian assemblages in the Algarve coast is apparent, at current rates, scuba diving does not seem to seriously affect gorgonians. However, this is a growing industry and the preference of scuba divers for natural rocky areas with diverse fauna is well known, which put these habitats under threat. The monitoring of scuba divers in the Algarve showed that most of them (88.6 %) have behaviours that can impact the habitat, presenting a mean contact rate of 0.340 ± 0.028 contacts min^{-1} ($\pm$SE). This rate was higher in scuba divers with moderate experience, and in the initial part of the dive (0–10 min). Contacts with fins and hands were common, mainly resulting in sediment re-suspension, but generally presenting low impact. However, fauna was also affected by physical damage and interactions, and under a scenario of significant expansion of this activity, the impacts on local fauna may increase with consequences for the sublittoral rocky ecosystems of the Algarve coast. Overall, the information gathered in this thesis, most of it completely new for the region, is expected to have a major contribution for the management of the Algarve coast.

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Introduction

I.1. Gorgonians

Morphology and systematics

Cnidaria are one of the most conspicuous faunal groups in marine ecosystems, with species occupying a diversity of habitats from the intertidal zone to abyssal plains (Daly et al., 2007). The class Anthozoa, a monophyletic clade from the phyllum Cnidaria, comprises solitary, clonal or colonial polypoid organisms, with approximately 7500 extant species (Daly et al., 2007). Anemones, corals, seapens and seafans are just some examples of groups of anthozoans that are commonly found in marine habitats.

The class Anthozoa is comprised by two main monophyletic groups: the Hexacorallia, all scleractinian and black corals, tube anemones, and sea anemones (≈ 4300 species); and the Octocorallia, soft corals, gorgonians (sea fans, sea whips), sea pens, and blue coral (≈ 3000 species) (Daly et al., 2007). According to Bayer (1981), gorgonians are octocorals with a supporting skeletal axis belonging to the order Alcyonacea (Daly et al., 2007), that presents two morphologically separated suborders, the Calcaxonia and the Holaxonia. Even though many families and genera require extensive taxonomic revision (McFadden et al., 2006; Daly et al., 2007), several famillies are widely distributed and speciose, namely Primnoidae, Isididae, Elisellidae, Plexauridae, Gorgoniidae, and Acanthogorgiidae (Daly et al., 2007).

Gorgonians are common and conspicuous in reef areas around the world (Etnoyer et al., 2010). These organisms possess an internal axial organic skeleton (proteinaceous material known as gorgonin, a tanned collagen or calcite) secreted by the coenenchyme, essentially to provide efficient filtering of food particles and to withstand strong currents (chapter 14, Ehrlich, 2010). Additionally, sclerites (mainly of calcite) compose the internal skeleton supporting and maintaining the shape of the organism, but are also important for protection, anchorage for the musculature and mineral storage (Fautin and Mariscal, 1991). Gorgonians are modular organisms, i.e. each individual (a colony) is formed by multiple units (modules), the polyps, distributed over the coenenchyme (mesoglea) around the gorgonian axis. Octocoral polyps are mainly composed by the coelenteron (gastric cavity), which is radially divided by eight mesenteries, the stomodeum (pharynx), a tube of tissue extending from the mouth to the coelenteron, the oral disk and pinnatelly branched tentacles that protrude from the oral disk between the mesenteries (Fautin and Mariscal, 1991). Polyps are interconnected by the existence of numerous stem canals and solenia in the coenenchyme that are used for food and water transport (Fautin and Mariscal, 1991). The mesenteries have several functions, namely related to reproduction, digestion and circulation (Fautin and Mariscal, 1991).

The ecological role of gorgonians

Gorgonians are long lived sessile colonial organisms, often presenting slow growth and low dynamics (Coma et al., 1998b; Garrabou and Harmelin, 2002; Linares et al., 2007, 2010). Because of their modular nature and internal skeletons that provide both stability (calcite) and flexibility (gorgonin) (Ehrlich, 2010) gorgonians can attain large sizes (Fautin and Mariscal, 1991), and persist for long periods of time in benthic marine habitats. Similarly to hard corals, gorgonians can be considered as ecosystem engineers as they "directly or indirectly modulate the availability of resources (other than themselves) to other species" and "modify, maintain and/or create habitats" (Jones et al., 1994). Their three-dimensional structure in the benthic realm provides niches that can be used or occupied by other species (physical engineering). What is more, their presence may also facilitate the colonization of space by other species (Begon et al., 2006). Erect sessile organisms with complex three-dimensional structures, when sufficiently dense, can decrease water movements and enhance finer sediments accumulation (Bruno and Kennedy, 2000), creating a gradient of environmental conditions that can be efficiently used by other species (Cerrano et al., 2009). Within gorgonian gardens, the effects of such role are for example increased biodiversity and faunal biomass (Linares et al., 2007; Cerrano et al., 2009), which can persist and be relevant over long temporal scales from decades to centuries (Cerrano et al., 2009).

In marine habitats, several species are associated with gorgonians. Filter-feeders hold to gorgonian branches while feeding, some species predate on their polyps and others use the gorgonian for protection (Krieger and Wing, 2002; Buhl-Mortensen et al., 2010). Fish are commonly found in the vicinity of gorgonians (Figure I.1) (Wolff et al., 1999; Buhl-Mortensen et al., 2010), sometimes at very short distances (less than one fish length; Bright, 2007) and the composition of fish assemblages has been found to be related to the presence of gorgonians (Gratwicke et al., 2006). Moreover, both adults and juveniles of important commercial species (fish and crustaceans) have been found to be associated with dense gorgonian gardens (Stone, 2006). Even though fish normally do not feed on gorgonians due to chemical defence by secondary metabolites (O'Neal and Pawlik, 2002), the butterflyfish *Chaetodon capistratus* is known to feed on the polyps of gorgonians, especially of the larger colonies (Lasker, 1985). Other fish species, such as the goby *Bryaninops amplus*, use gorgonians for protection, but this effect is dependent of colony height and gorgonian architecture and fish size is limited by colony width (Sih and Chouw, 2009).

In the coralligenous assemblages of the Mediterranean Sea, gorgonians are considered important "engineering" or foundation species (Mistri and Ceccherelli, 1994; Linares et al., 2005; Coma et al., 2006; Linares et al., 2008a,d; Cupido et al., 2009; Gori et al., 2011b; Huete-Stauffer et al., 2011). Setting the ecological attributes of a species under theoretical frameworks and concepts sometimes results in confounding those concepts. Gorgonians are probably better defined as biogenic or foundational species as they create biogenic habitats. Regardless the term used to

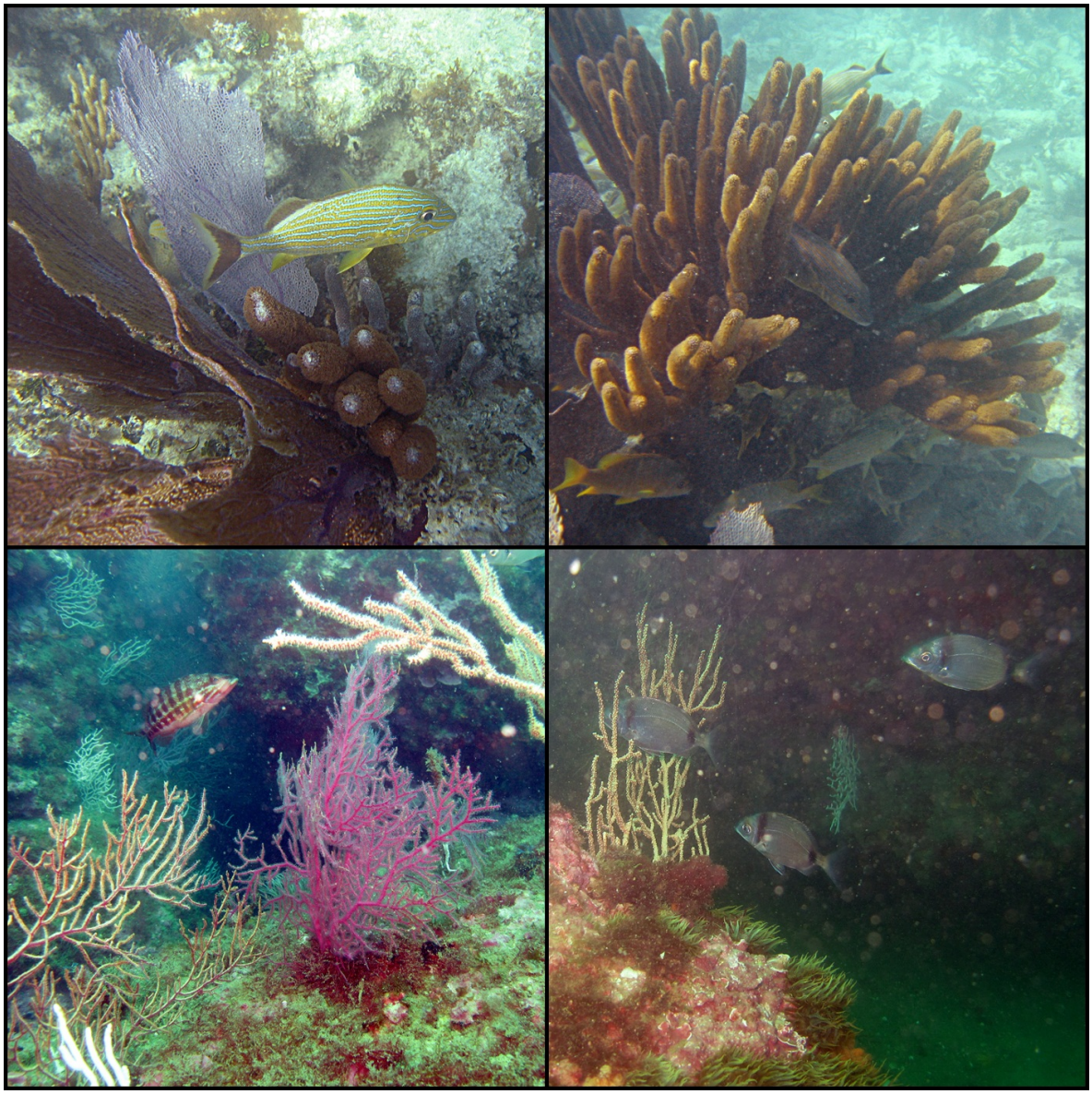

Figure I.1.: Fish using the habitat provided by gorgonians. **top-left**: bluestriped grunt (*Haemolum sciurus*) sheltering near a *Gorgonia ventalina* colony (Mexico); **top-right**: a small group of bluestriped grunts passing nearby a *Plexaura* sp. colony used by one individual of the same species (Mexico); **bottom-left**: *Serranus atricauda* slowly swimming close to *Leptogorgia lusitanica*, *Leptogorgia lusitanica* and *Eunicella labiata* colonies (Pedra da Greta, Algarve); **bottom-right**: *Diplodus sargus* calmly swimming by a *Eunicella labiata* colony. All photos by João Cúrdia.

classify these organisms, the scale of the effects of "engineering" or foundation species depends greatly on their density, spatial distribution and capacity per capita (depending on size for benthic suspension feeders) (Jones et al., 1997). Therefore, all the factors impacting local and regional populations of foundation species are likely to affect their associated species (Meadows et al., 2012) and ultimately their ecological role.

Goods and services associated with gorgonians

Similarly to coral reefs, gorgonian gardens may provide an array of goods and ecological services that are summarized in Table I.1. Therefore, it is essential to acknowledge the goods and services provided by those specific habitats in order to shed light on the associated cost of loosing or restore them in the future (Barbier, 2012).

In recent years the demand for natural bioactive compounds by the pharmaceutical industry led to many investigations concerning gorgonian compounds, especially because many gorgonians present chemical defence against predators (e.g. Van Alstyne and Paul, 1992; Koh et al., 2000; O'Neal and Pawlik, 2002; Changyun et al., 2008) and disease agents (e.g. Kim et al., 2000; Shapo et al., 2007). From 1998 to 2009, a total of 263 scientific articles were published in peer reviewed journals concerning gorgonians (http://isiwebofknowledge.com). The majority of those articles (173; 65.8 %) were related to bioactive compounds isolated from these organisms, many of them new to science. With respect to gorgonian species occurring in the south of Portugal, bioactive compounds have been extracted from *Leptogorgia sarmentosa* (Garrido et al., 2000; Boonananwong et al., 2008) and *Eunicella labiata* (Roussis et al., 1996). The remaining species from the Portuguese coast, to the author best knowledge, have not been screened for bioactive compounds, and therefore remain as potential sources of new chemical products. Some of those compounds may prove valuable for human health as antitumoral, anti-inflamatory, antimalarial, antimicrobial and antituberculosis agents (Bhakuni and Rawat, 2005; Ioannou et al., 2008; Berrue and Kerr, 2009; Rocha et al., 2011). Some diterpenoids and pyridines can also be an ecological alternative to the banned chemical anti-fouling agents (Qian et al., 2010; Rocha et al., 2011), as the fouling of human made structures in the sea represents significant costs especially concerning shipping (Schultz et al., 2011).

In the Algarve, the scuba diving industry has been growing in the past few years (Santos et al., 2006). Together with large sized fishes and shoals, and commercial shellfish species, gorgonian gardens are considered the top features of a good diving spot in the region. Even though not evaluated at present, healthy gorgonian gardens per se may add value to the region, especially if the scuba divers are aware of the ecological relevance of gorgonians as they already value the aesthetics and structure provided by seascapes characterized by large colonies and high density and diversity of gorgonians (Rodrigues, 2008).

Table I.1.: Goods and ecological services of gorgonian gardens. Adapted from Moberg and Folke, 1999.

Goods	**Ecosystem services**				
Renewable resources	Biotic		Biogeochemical	Information	Social and cultural
	Within habitats	*Between habitats*			
Sea food products	Maintenance of habitats	Biological support through "mobile links"	CO_2/Ca budget control	Monitoring and pollution record	Support recreation
Raw materials for medicine	Maintenance of biodiversity and a genetic library		Waste assimilation	Climate record	Aesthetic values and artistic inspiration
	Biological maintenance of resilience				Sustaining the livelihood of communities
	Regulation of ecosystem processes and functions				

Due to their ecological role mentioned above, gorgonians may also provide increased fishing yield, as some commercial fish species are associated to gorgonian habitats (Wolff et al., 1999), but also because they may provide the links between fish habitats (Moberg and Folke, 1999) functioning as "stepping stones".

I.2. Algarve underwater: threatened natural heritage

The Algarve coast

The Algarve region comprises an area of 4996.8 km with its coastline extending for 320 km (www.ine.pt). The coast presents a high diversity of features, such as abrupt and jagged coastlines, extensive sandy beaches, salt marshes, sand dunes and inlets forming lagoons (INAG, 2011). In general, the western coast of the Algarve (Barlavento) is characterized by rocky formations of several types (e.g. underwater spurs, boulders, smooth rocky plateaus) and different sediment dynamics. In the eastern coast (Sotavento), the shallow sublittoral area (down to 30 m depth) is characterized by low relief sandy areas and rocky bottoms are scarce. From Cabo Santa Maria (near Faro, central part of the Algarve) to Vila Real de Santo António (bordering Spain), there are only two large rocky areas, Pedra da Greta and Pedra do Barril. Apart from these two areas, only small rocky reefs (less than 200 m in length) can be found scattered over the large sandy areas. The scarcity of rocky bottoms led to the deployment of large sized artificial reefs off the southern coast from 1990 to 2003 (Santos et al., 2011) for fisheries and conservation purposes. According to Fabi et al. (2011), the overall artificial reef complex consists of more than 21 500 concrete modules, occupying, in a discontinuous way, a total area of 43 km.

The climate in the region is temperate with average maximum air temperature ranging from 16.1 (January) to 29.0 °C (August) (Instituto de Meteorologia, 2012). Sea breezes prevail for 70 % of the year in the south coast of Portugal, characterized by low wave action during the day rising to about 1 m height waves from SW at sunset decreasing to less than 0.5 m during the night, generally with weak residual waves from the SW during the day (Pires, 1985). Storms from SW (64 %), especially during winter, are the most energetic wave conditions in the Algarve, with waves frequently higher than 6 m (Costa et al., 2001). Storms from SE (32 %) can generate waves up to 5 m with short period and associated to strong winds from SE (Costa et al., 2001). The tidal regime is semi-diurnal and mesotidal with tides ranging from 1.36–2.70 m during neap tides and from 0.64–3.82 m during spring tides (Moura et al., 2006). In general, the circulation patterns in the Iberian Peninsula are dominated by up-welling (summer) and down-welling (winter) events associated to northerly and southerly winds, coupled to the North Atlantic Oscillation (Sánchez et al., 2007). The coastal flow along the SW Iberian Peninsula has an alternating nature, featuring sharp current

inversions on time scales of less than 2 days (Relvas et al., 2007), with a dominant alongshore flow on the inner shelf (Sánchez et al., 2006). Topological features, such as the submarine canyon of Portimão and the Cape São Vicente provide instability, forming eddies that change the circulation patterns at the mesoscale (Cherubin et al., 2000).

Benthic communities of Algarve sublittoral rocky areas

The shallow sublittoral coastal rocky habitats of the Algarve (<30 m) have been poorly studied until recently (Gonçalves et al., 2004, 2007, 2010). The shallow rocky areas of the region can be divided in two main groups, rocky areas extending from the shore and isolated rocky formations of variable dimensions. In the Sotavento, only the latter group occurs. In the Algarve the sublittoral rocky areas have Atlantic and Mediterranean affinities and are subjected to moderate energy (according to the European Nature Information System – EUNIS criteria). The benthic habitats present an abundant and diverse flora dominated by red algae covering the rocky surfaces (*Mesophyllum* spp., *Lithophyllum* spp., *Lithothamnion* spp., and *Peyssonelia* spp.) forming banks of coralligenous frameworks, with some erect algae (mostly from genera *Halimeda* and *Flabellia*) (Gonçalves et al., 2004, 2007, 2010). The invertebrate community is diverse with several species of Gastropoda and a wide array of suspension feeders (gorgonians, sponges, hydrozoans, serpulids and tunicates) (Gonçalves et al., 2004, 2007, 2010). The fish communities in rocky areas are also diverse being dominated by Sparidae, Labridae and Gobiidae (Gonçalves et al., 2007, 2010).

Three biotopes have been described (Gonçalves et al., 2007, 2010) regarding the faunal communities of these habitats: coastal and deep infralittoral rock (EUNIS A3.24); and circalittoral rock (EUNIS A4.27). The coastal infralittoral rock (depth <9 m) is mainly dominated by algae (*Halopteris filicina*, *Litophyllum incrustans*, *Corallina elongata*, *Cystoseira* spp., *Plocamium cartilagineum*, *Dictyota dichotoma* and *Asparagopsis armata*), but also presents invertebrate fauna, such as the cnidarian *Anemonia sulcata*, the sponge *Phorbas fictius* and herbivores like the gastropod *Gibbula cineraria* and the sea urchin *Paracentrotus lividus*. In the deep infralittoral biotope (9–21 m depth), algae are less dominant, but *Litophyllum incrustans* and *Dictyota dichotoma* are still characteristic, as well as several suspension feeding species such as the sponges *Phorbas fictitius* and *Cliona viridis*, the bryozoans *Turbicellopora* spp. and *Myriapora truncata* and the gorgonians *Eunicella gazella* and *Eunicella verrucosa*. Gastropod species (*Bolma rugosa* and *Hexaplex trunculus*) and the cnidarians *Anemonia sulcata*, *Aiptasia diaphana* and *Corynactis viridis* are also abundant (Gonçalves et al., 2007, 2010). In the circalittoral rocky areas (21–30 m depth) the benthic communities are dominated by animals, namely conspicuous invertebrates, such as the gorgonians *Eunicella labiata*, *Eunicella verrucosa*, *Eunicella gazella* and *Leptogorgia sarmentosa*, the sponges *Phorbas fictius*, *Axinella polypoides*, *Cliona viridis* and *Crella fusigera* and the bryozoan *Pentapora foliacea* but also smaller organisms, such as the anthozoans *Parazoanthus*

axinellae and *Alcyonium acaule* and the bryozoan *Myriapora truncata* (Gonçalves et al., 2007, 2010).

In the Algarve, the deep infralittoral and especially the circalittoral rocky areas are dominated by dense gorgonian gardens composed by several species, namely *Eunicella labiata*, *Eunicella verrucosa*, *Eunicella gazella*, *Leptogorgia sarmentosa* (Gonçalves et al., 2010) and *Leptogorgia lusitanica*.

According to the works by Grasshoff (1972, 1977, 1988, 1992); Carpine and Grasshoff (1975); Vieira (2008) the gorgonian fauna reported for the Algarve waters to 100 m comprise the following species:

- Suborder: **HOLAXONIA**
  - Family: **GORGONIIDAE**
    - *Eunicella gazella* Studer, 1878
    - *Eunicella labiata* Thompson, 1927
    - *Eunicella singularis* (Esper, 1791)
    - *Eunicella verrucosa* (Pallas, 1766)
    - *Leptogorgia lusitanica* Stiasny, 1937
    - *Leptogorgia sarmentosa* (Esper, 1789)
    - *Leptogorgia viminalis* (Pallas, 1766)
  - Family: **PLEXAURIDAE**
    - *Spinimuricea atlantica* (Johnson, 1862)
    - *Spinimuricea klavereni* (Carpine & Grasshoff, 1992)
    - *Paramuricea macrospina* (Koch, 1882)

Natural and anthropogenic impacts in the Algarve coast

Unfortunately, natural and anthropogenic pressures threaten the health of gorgonian gardens, jeopardising the benefits deriving from the services and goods that they provide.

The human population in the Algarve (residents) is increasing since the 1970s (CCDR Algarve, 2011d; Instituto Nacional de Estatística, 2011) and in the period between 2001 and 2009 presented a mean population growth of 1.31 % (Carrilho and Patrício, 2010) attaining in 2009 a population of ≈434 000 and a mean density of 86.9 inhabitants km^{-2} (INE, 2010). Furthermore, the Algarve population increases dramatically during summer due to tourism (CCDR Algarve, 2011f). The systematic natural and seasonal increase in population led to the development of several infrastructures, to higher consumption of energy and water (CCDR Algarve, 2011b,a) and to increased production of waste (e.g. urban solid residues showed an increasing trend from 1999 to 2006; CCDR Algarve 2011e). The local authorities have been carrying out plans to improve the coastal zone management, namely the POOC (Planos de Ordenamento da Orla Costeira) aiming at preventing or reducing impacts. However, most of the invested funds were applied in the re-qualification of beaches (nourishment of beaches with dredged sediments) and defensive infrastructures (such as spurs, e.g. Vilamoura) and only a small part was applied in ground-base and monitoring studies (CCDR Algarve, 2011c).

The Algarve has a long tradition of fishing, a relevant socio-economical activity including several important fisheries, such as the sardine, crustaceans and tuna (Oliveira das Neves, 2000; Galvão, 2008; Mata, 2009). However, conservation actions have focused primarily on inland habitats in tune with international laws and directives (Habitats Directive, Birds Directive, Natura 2000). As a result, in the southern Algarve coast only Ria Formosa, Ria de Alvôr (Protected Areas) and the Martinhal islets (off Sagres, partially protected) present restrictions to fishing and therefore, the whole coast is subjected to fishing, even though with varying intensity. Consequently, rocky areas are intensively exploited by professional and recreational fishermen because they usually present highly appreciated and valued fish and shellfish species. Angling lines, pots, traps, trammel nets, gill nets, purse seine are commonly used fishing gear in the Algarve (e.g. Erzini et al., 1997; Santos et al., 2003a; Erzini et al., 2008; Gonçalves et al., 2008; Veiga et al., 2010). These are often set on or nearby rocky substrata. Storms, or other random events (e.g. interaction between passive and active fishing gears) can displace fishing gears on the seafloor where they easily become entangled in the various features of the rocky bottom, such as large rocks, overhangs and spurs but also on conspicuous living fauna such as large sponges, gorgonians and bryozoans. "Ghost fishing" (mortality of marine fauna caused by the accidental entanglement in lost fishing gear) can be a matter of concern in the Algarve as an estimated total of 1782 gill and trammel nets is lost every year in the Algarve coast. The local fleet (vessels with <9 m) operating mainly close to the coastline, up to 3 M and at depths lower than 50 m is responsible for 79 % of these lost gear and nearly a quarter of the fishing traps are lost during fishing operations (Erzini et al., 2008).

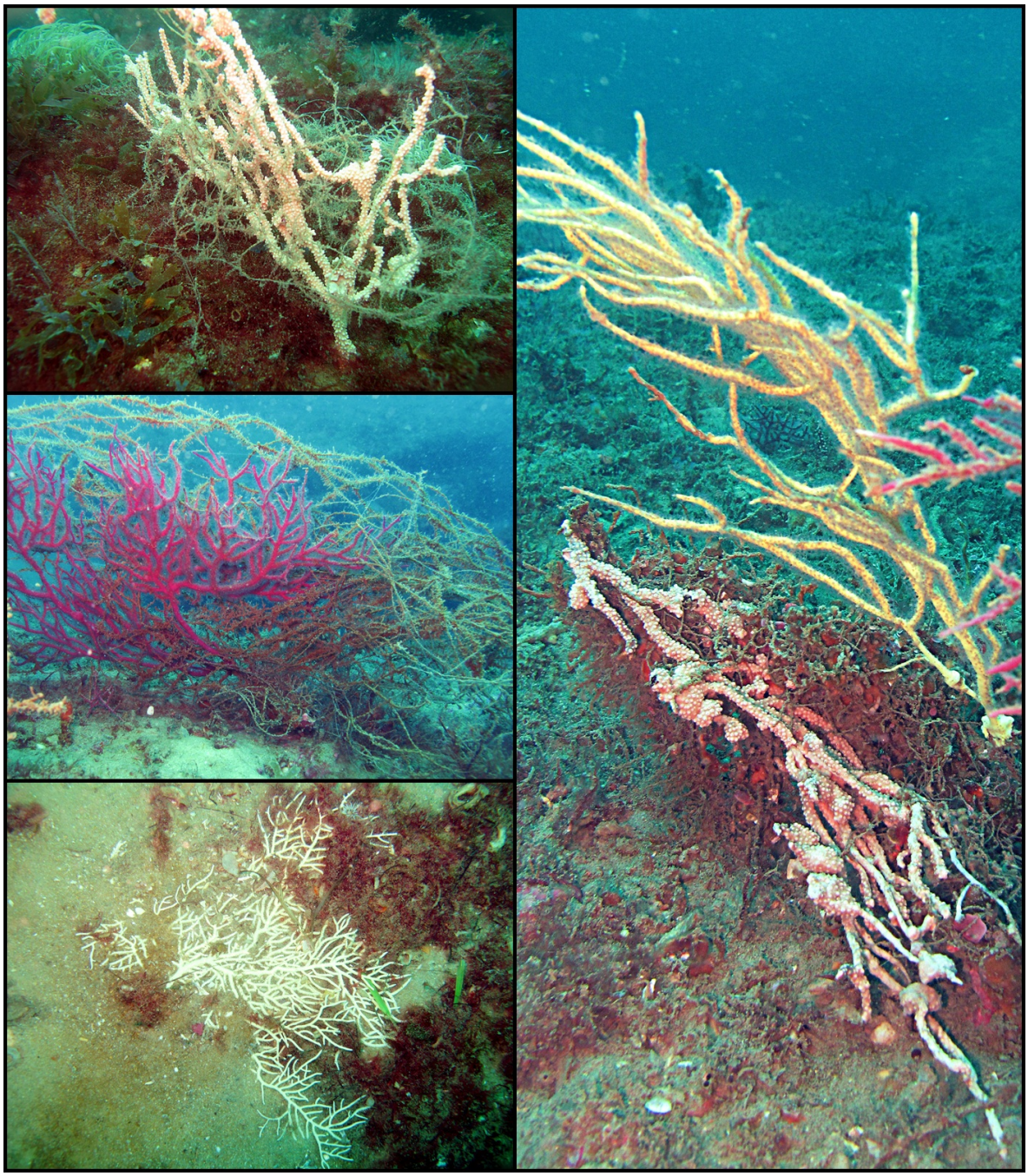

Figure I.2.: Gorgonians affected by fishing gears. **top-left**: *Eunicella labiata* entangled in a gill net; **center-left**: *Leptogorgia sarmentosa* covered by a gill net; **bottom-left**: *Leptogorgia sarmentosa* detached from the substrate, sediment will suffocate the colony; **right**: *Eunicella labiata* entangled in lost fishing gears, a trammel net, the weight of the fishing gears completely bended the colony. All photos by João Cúrdia.

The impacts associated with fishing, either direct or indirect, affect the sessile benthic communities, namely gorgonians (e.g. Willison et al., 2000; Eno et al., 2001; Morgan and Ratana, 2003; Shester and Micheli, 2011). Not surprisingly, gorgonians are commonly collected in the Algarve by fishermen while retrieving fishing gears (Nobre, 1931; Gonçalves et al., 2008; Vieira, 2008). In fact, detachments from the substratum (Figure I.2) and injuries are the main causes of gorgonian mortality (Weinberg, 1978; Coma et al., 2004; Linares et al., 2008d). This can be a severe threat if generalized within a population or community because the recovery of detached gorgonians seems to be low (Linares et al., 2008d). On the other hand, because of the long life span of lost fishing gears materials, "ghost fishing" can also inflict substantial damage to sessile organisms, namely gorgonians (Morgan and Ratana, 2003). The soft tissues of entangled gorgonians are subjected to long and continuous abrasion, damaging the animals, exposing them to disease and forcing the colony to allocate energy for regeneration purposes, normally as a trade-off on growth or reproduction (Wahle, 1983; Rinkevich, 1996; Henry and Hart, 2005).

Anchoring can also impact rocky bottom's fauna (Milazzo et al., 2002; Davenport and Davenport, 2006; Lloret and Riera, 2008), while casting and uncasting the anchor. In the former, the anchor may dwell on the rocky bottom destroying any structure that is found in its track. Furthermore, if the anchor becomes firmly fixed to the bottom, boat skippers tend to accelerate the engine to release the anchor, increasing the torque and often breaking the structure holding the anchor. Scuba diving may also affect gorgonians due to breakage or detachment, abbrasion of the coenenchyme, reduced reproduction and feeding constraints (Coma et al., 1995; Garrabou et al., 1998; Luna et al., 2009; Tsounis et al., 2012). The consequences of such damages are similar to those mentioned for fishing.

The challenge of understanding the processes governing global warming is currently one of the most demanding scientific issues, due to its impacts on human societies and also on the environment and the biodiversity (Hoegh-Guldberg and Bruno, 2010, and references therein). Mass mortality events of benthic species have been linked to global warming and are well documented, both for coral reef ecosystems (e.g. Hughes et al., 2003; Hoegh-Guldberg et al., 2007; Hughes et al., 2010) and for Mediterranean benthic assemblages (e.g. Linares et al., 2005; Coma et al., 2009; Garrabou et al., 2009; Previati et al., 2010). Solid evidence linking anomalous high temperatures in the Mediterranean Sea to abnormal mortality of several benthic species has been gathered, namely concerning gorgonians (Schiaparelli et al., 2007; Huete-Stauffer et al., 2011). The increase of temperature affects the metabolism of some gorgonian species; it increases the oxygen consumption up to a temperature threshold and dramatically reduces polyp activity afterwards (and also oxygen consumption), leading to necrosis and colour change, thus severely affecting the biology of these animals (Previati et al., 2010). Such catastrophic events affect primarily the density, growth and reproduction of gorgonian species (Linares et al., 2008c), leading to severe changes in species composition and community structure of coralligenous communities (Coma et al., 2006).

I.3. Objectives and the branching and modular nature of the thesis

Aiming at contributing to a better knowledge on the ecology and biology of gorgonian assemblages in the southern coast of Portugal, and to contribute to their future conservation, several studies were designed and undertaken that make part of this thesis. Specifically, the present thesis aims to: 1) characterize the distribution patterns of gorgonians, their variability in the region and the possible causes of such variability; 2) estimate the biodiversity that is associated with gorgonians and investigate the factors determining diversity patterns of attendant epifaunal assemblages; 3) study the reproductive cycle of a frequent and abundant gorgonian and 4) assess the impacts of scuba diving in the region. The thesis is organized in four parts, each addressing one of the main objectives of the thesis.

The first part comprehends two chapters. In chapter 1, the abundance and frequency of the main gorgonian species in shallow rocky bottoms are analysed over 25 km of coastline from 0 to 30 m to determine the spatial variability at the local scale. In chapter 2 the following questions are addressed: i) what are the main distribution patterns of gorgonians along the southern coast of Portugal?; ii) are there differences in structure and composition of the assemblages under different intensity of disturbance?; iii) can size-frequency distributions of dominant species be used as a proxy to assess the vulnerability of the assemblages?

Part II focuses the fauna that can be found living on gorgonian colonies from the Algarve. Chapter 3 aims to investigate if i) different gorgonian species and ii) colonies of different size present different epifaunal assemblages (composition and structure) and if those patterns are consistent in space and time. In chapter 4, the effects of colony area, structural complexity, epibiont cover on the diversity and abundance of the attendant fauna of *Leptogorgia lusitanica* and *Eunicella gazella* are investigated. In this chapter, it is also investigated how different taxonomic or functional groups, with different habitat requirements, respond to gorgonian attributes.

The study on the reproductive biology of *Eunicella gazella* presented in chapter 5, the first for this species, aims to characterize the oogenic and spermatogenic cycles of this common species in the Algarve, and estimate its fecundity and spawning period.

Chapter 6 aims to characterize the impacts of scuba diving in the Algarve, investigating also if scuba diver experience and the time of dive influence the rate of contacts and the associated impacts to the habitat and fauna.

Finally, and because the information provided by the several studies is of different nature, the main results are integrated into general conclusions. It is also discussed how the results and conclusions can be used for management purposes and pointed out some future research.

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Part I.

Gorgonian assemblages in the Algarve coast

CHAPTER 1

Spatial and depth-associated distribution patterns of gorgonians in temperate NE Atlantic shallow rocky bottoms

Submitted to: *Helgoland Marine Research*

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Abstract

The ecological role of gorgonians for marine rocky bottoms is worldwide recognized, but the information on the distribution patterns of NE Atlantic temperate species is insufficient, considering current global, regional and local threats. To overcome the lack of information on the spatial distribution patterns of gorgonians in south Portugal, in 2009/2010 the occurrence and abundance of gorgonian species in rocky bottoms were quantified over more than 25 km of coast (37.1°N/8.6°W) down to 30 m depth. *Eunicella labiata*, *Eunicella gazella*, *Eunicella verrucosa* and *Leptogorgia sarmentosa* were abundant and frequent in the studied area, while *Leptogorgia lusitanica* was less abundant. All species evidenced a similar depth pattern, i.e. abundance significantly increased with depth below 15 m. At shallower waters (up to 15 m), the distribution of gorgonians may be constrained by abiotic factors and competition with algae. Indeed, the abundance of gorgonians was negatively correlated with the percentage cover of algae along the depth gradient, but competition between gorgonians and sponges was not apparent. Competition among gorgonian species also seems to be low in this area because of the similarity in the abundance pattern observed for the most abundant species and also their high association. In NE Atlantic shallow temperate rocky bottoms, the distribution of gorgonians seems to be influenced by environmental factors and biological interactions, namely competition with algae.

Keywords: gorgonians • *Leptogorgia* • *Eunicella* • spatial distribution • rocky bottoms • biological interactions

1.1. Introduction

Gorgonians (Octocorallia: Alcyonacea) are colonial organisms characterized by a hard skeleton, slow growth and long life span. Their three dimensional structure may modify the physical habitat, by reducing current velocity, stabilising soft substrata, enhancing sedimentation and local accumulation of fine particles (Bruno and Kennedy, 2000), as well as increasing availability of niches. Because gorgonians are long-lived animals they may extend these modifications for long time, producing significant effects in marine ecosystems, namely by enhancing local diversity (Cerrano et al., 2009). These animals are considered as ecosystem engineers (sensu Jones et al., 1994, 1997), whose ecological role in ecosystem functioning has been widely acknowledged (Ballesteros, 2006; Coma et al., 2006; Cupido et al., 2008; Linares et al., 2008d), with particular emphasis on their role in marine conservation (see Wright and Jones, 2006).

Over the last decades, many studies reported that gorgonians are affected by drastic, rapid

and lasting disturbances either of natural (Martin et al., 2002; Linares et al., 2005; Coma et al., 2006; Schiaparelli et al., 2007; Garrabou et al., 2009) or human origin, such as fishing (mainly bottom trammel/gill nets, bottom seine and bottom trawl) (Bavestrello et al., 1997; Willison et al., 2000; Chiappone et al., 2002, 2005), pollution (Bruno et al., 2003; Cerrano and Bavestrello, 2008), anchoring and scuba diving (Coma et al., 2004; Linares et al., 2008d). Detailed knowledge on the distribution patterns of abundance of each species is essential to detect the human footprint in marine ecosystems and propose adequate and achievable conservation and management measures (Benedetti-Cecchi et al., 2003; García-Charton et al., 2008; Costello et al., 2010).

The Algarve coast (southern Portugal, north-eastern Atlantic) presents a rich fauna with biogeographic affinities with the Mediterranean Sea, the Lusitanian, the west African Transition, Northern European Seas and Western Atlantic provinces (sensu Spalding et al., 2007; Souto et al., 2010; Levy et al., 2011), because of the proximity to the Strait of Gibraltar (Baus et al., 2005, and references therein) and the confluence of oceanic currents (Cherubin et al., 2000; Pérez et al., 2001; Coelho et al., 2002; Martins et al., 2002). However, the gorgonian populations of southern Portugal are poorly described, especially compared to the Mediterranean, where in the past few years, several studies have been performed in shallow sublittoral waters, gathering a large amount of biological and ecological information, and building predictive models to be used in conservation plans (Linares et al., 2007, 2008d; Bramanti et al., 2009). In fact, the most recent study concerning the gorgonian fauna of the Algarve coast reported only 10 different species caught as by-catch by bottom gill nets (Vieira, 2008). Therefore, significant knowledge gaps still persist, namely on the abundance patterns in the near shore benthic community (0–30 m), spatial and depth distribution.

In this context, the present study aimed to quantify the occurrence and abundance of the main gorgonian species in the shallow rocky bottoms (0 to 30 m) of the western Algarve coast (≈25 km of coastline). In order to assess the relationship between the distribution of gorgonians and potential competitors for space and food, the percentage cover of erect algae and Porifera were also quantified. If population dynamics of those benthic taxa is governed by competition, it is expected that the abundance of gorgonians and both erect algae and Porifera would be inversely correlated.

1.2. Materials and Methods

1.2.1. Study area

The Algarve coast (Figure 1.1) is characterized by heterogeneous coastline and sublittoral areas. The western part of the Algarve coast comprises rocky formations of several types (e.g.

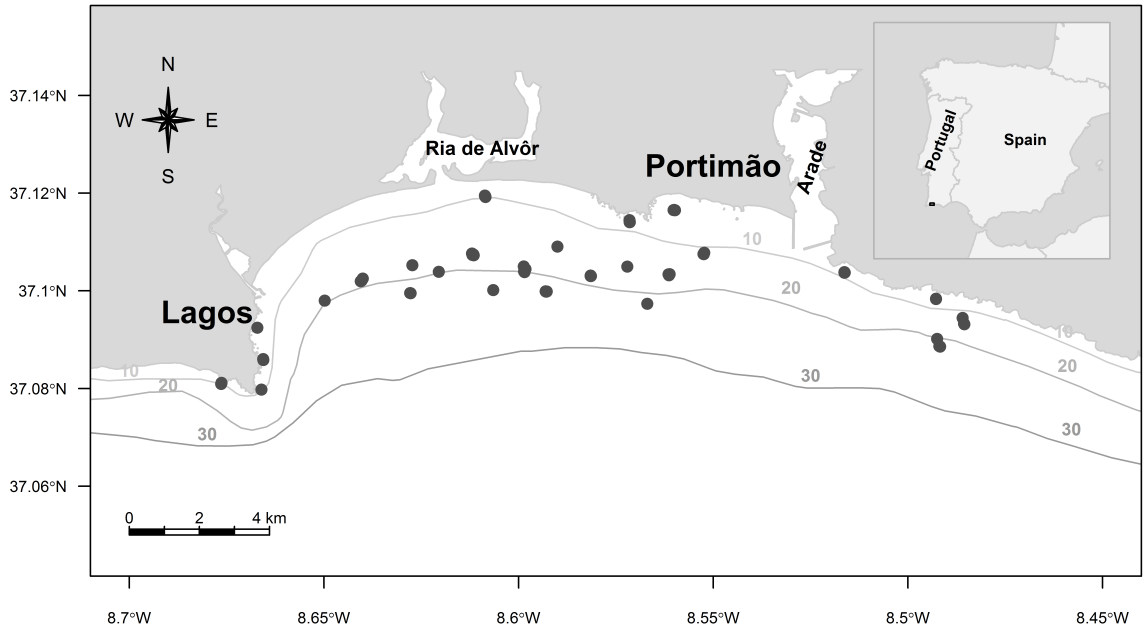

Figure 1.1.: Location of the sampling sites (•) in Lagos Bay.

underwater spurs, boulders, low relief rocky areas, submerged rock bottoms) and by different sediment dynamics.

The study area is located in the western Algarve coast extending from Lagos to Portimão (Figure 1.1), hereafter designated by Lagos Bay. This area has 20.6 km^2 of rocky bottoms within a total area of 70 km^2 (up to 30 m depth) and covers ≈25 km of the Algarve coast, distancing only ≈30 km to the westernmost continental part of Europe (Cabo São Vicente, Sagres). In particular, the coast between Ponta da Piedade and Armação de Pêra, where this study was conducted, is morphologically complex presenting rocky areas with cliffs forming small beaches, a large bay with extensive sandy beaches and dunes, including a coastal lagoon (Ria de Alvor) and a small estuary (Rio Arade). The shallow continental shelf (down to ≈30 m depth) is generally characterized by rocky outcrops with pockets of rubble and/or sand (Gonçalves et al., 2010).

In general, the circulation patterns in the Iberian Peninsula are dominated by up-welling (summer) and down-welling (winter) events associated to northerly/southerly winds, coupled to the North Atlantic Oscillation (Sánchez et al., 2007). Sea surface temperature presents marked seasonal variation depending on whether down-welling or up-welling dominates (ranging from 14 to 24°C, respectively; http://www.hidrografico.pt/), whereas salinity is fairly constant (35.0–36.0).

1.2.2. Species identification

Identification of gorgonian species was based on the studies by Carpine and Grasshoff (1975), Grasshoff (1988, 1992) and González (1993). In the Algarve coast, underwater identification of gorgonians is difficult because of ambiguities in the taxonomy of *Eunicella* and *Leptogorgia*, and therefore the following criteria were established to identify these species:

Eunicella gazella – colonies always white with orange polyps; diameter of the ramets noticeably larger than in *Eunicella verrucosa*; colony surface generally homogeneous with low relief and extensive branching mostly in one dimension.

Eunicella verrucosa – colonies with colour varying from white to cream, beige or pale orange; polyps varying from white to orange; heterogeneous surface with "bumps" (verrucae), usually larger in size than *Eunicella gazella*.

Eunicella labiata – large species; colonies divided in two main branches immediately after the base of the colony, with less branches than *Eunicella verrucosa* and *Eunicella gazella*; colours are usually darker than in the previous species, ranging from cream to dark brown; colonies are often broken, loosing one of the main branches; conspicuous verrucae observed all over the colony, usually lighter.

Eunicella singularis – erect colonies with few long branches always in upright position; colonies always white coloured; colony surface generally smooth with low relief.

Leptogorgia lusitanica – bush-like colonies growing in only one dimension, perpendicular to dominant currents; terminal branches thinner than the central ones; extremely variable in colour, generally presenting two colours, usually wine red/purple and yellow, sometimes white and blue, and other times uniform in colour (generally white or yellow); the central branches of the colony usually lack polyps in the surface facing the currents.

Leptogorgia sarmentosa – bush-like colonies growing in one or more dimensions; usually of uniform but variable colour (green, yellow, red, brick orange, rarely white); polyps usually present in all surfaces of the branches.

1.2.3. Spatial and depth distribution of the main gorgonian species

In order to describe the patterns of spatial and vertical distribution of gorgonian species, a total of 69 sites were sampled by means of underwater transects by scuba diving (5 × 1 m belt transects, 3 replicates at each site) from May 2009 to June 2010. Sampling sites were randomly selected,

but restricted to rocky substrata, explaining the spatial gaps. In this area, gorgonians are rarely found in soft bottoms, therefore sampling effort was directed towards rocky bottoms only. The bathymetric distribution of the gorgonian species was analysed considering the average depth of each sampling unit and estimating the median density at 6 depth levels: 0–5 m, 5–10 m, 10–15 m, 15–20 m, 20–25 m and 25–30 m.

1.2.4. Competition between gorgonians and other benthic groups

In order to assess competition effects between gorgonians and potential competitors for space and food, the abundance of erect algae (macroalgae and turf) and Porifera was quantified. While conducting the censuses of the gorgonian populations, the number of sponges was counted at each transect and the percentage cover of erect algae was quantified using quadrats (1×1 m, 3 replicates).

1.2.5. Statistical analyses

The distribution of gorgonian species indicated that only five out of seven species were frequent in the study area (see Results). Therefore, the comparison of the density of gorgonians at different depth levels was undertaken for the overall gorgonian assemblage (all gorgonians) and for the most frequent species (*Leptogorgia sarmentosa*, *Leptogorgia lusitanica*, *Eunicella gazella*, *Eunicella labiata* and *Eunicella verrucosa*) using parametric (one-way ANOVA) or non-parametric methods (Kruskal-Wallis' U test) whenever ANOVA assumptions were not met. In both cases, pairwise multiple comparisons were used: Tukey Honestly Significant Differences (Tukey HSD) and Behrens-Fisher non-parametric multiple test (Berhens-Fisher) (Munzel and Hothorn, 2001), respectively. The number of transects was not constant at each depth level, resulting in an unbalanced design, therefore depth levels with fewer samples (0–5 m and 25–30 m) were discarded to improve the power of the statistical tests. The correlation between depth and density of gorgonians was tested by means of an exponential regression using the $\log_e(1+y)$ transformation of the dependent variable.

Non-metric multidimensional scaling was used to analyse differences in the distribution and abundance patterns of gorgonian assemblages using the modified Gower dissimilarity index with transformed data ($\log_2(x+1)$). The modified Gower index (Anderson et al., 2006) is able to detect changes in composition, with the advantage of being directly interpretable as the average change in orders of magnitude (defined by the transformation). By using $\log_2$ transformation the modified Gower index is weighted towards a compositional change equal to a doubling in abundance (Anderson et al., 2006). To analyse the contribution of each species to the discrimination of the

compared assemblages, the indicator value (IndVal) was used (Dufrêne and Legendre, 1997). On the other hand, the ecological association of gorgonians was quantified using three measures based on binary data (presence-absence data): Ochiai, Dice and Jaccard (Janson and Vegelius, 1981). The three measures present minimum coexistence values of 0 when the two species are never found together and maximum coexistence values of 1 when both species always occur together (Janson and Vegelius, 1981).

The correlation between the abundance of gorgonians and potential competitors was assessed using linear regression. All statistical analyses were performed using the open source software R version 12.1 (R Development Core Team, 2010).

1.3. Results

1.3.1. Distribution patterns of gorgonian species

Occupancy and abundance

In Lagos Bay, gorgonians were present in 134 (64.7 %) of the 207 sampling units, totalling 2481 colonies belonging to seven taxa (Table 1.1). Four species, *Eunicella labiata*, *Eunicella verrucosa*, *Leptogorgia sarmentosa* and *Eunicella gazella*, were responsible for 96.9 % of the total abundance. *Eunicella labiata* was the most frequent and abundant species with 905 colonies, occurring in 52.7 % of the transects and representing 36.5 % of the total gorgonians found. *Eunicella verrucosa* was the second most frequent and abundant species with 22.4 % of the total abundance and occurring in 45.9 % of the transects. *Leptogorgia sarmentosa* was present in 39.6 % of the transects with 485 colonies (19.5 %). *Eunicella gazella* was found in 40.1 % of the transects contributing for 18.5 % of the total abundance. *Leptogorgia lusitanica* was found in 16.9 % of the transects and totalling 72 colonies (2.9 %). Only three colonies of *Eunicella singularis* were found in a single transect. One *Eunicella* colony (*Eunicella* sp.) could not be identified to species level.

Spatial and depth distribution

Generally, gorgonians were present in the entire study area, without any evidence of spatial segregation (Figure 1.2).

In Lagos Bay, gorgonians were found from 7.5 to 27 m (the maximum depth sampled). The depth range of all species presented similar upper limits, with *Leptogorgia sarmentosa* occurring

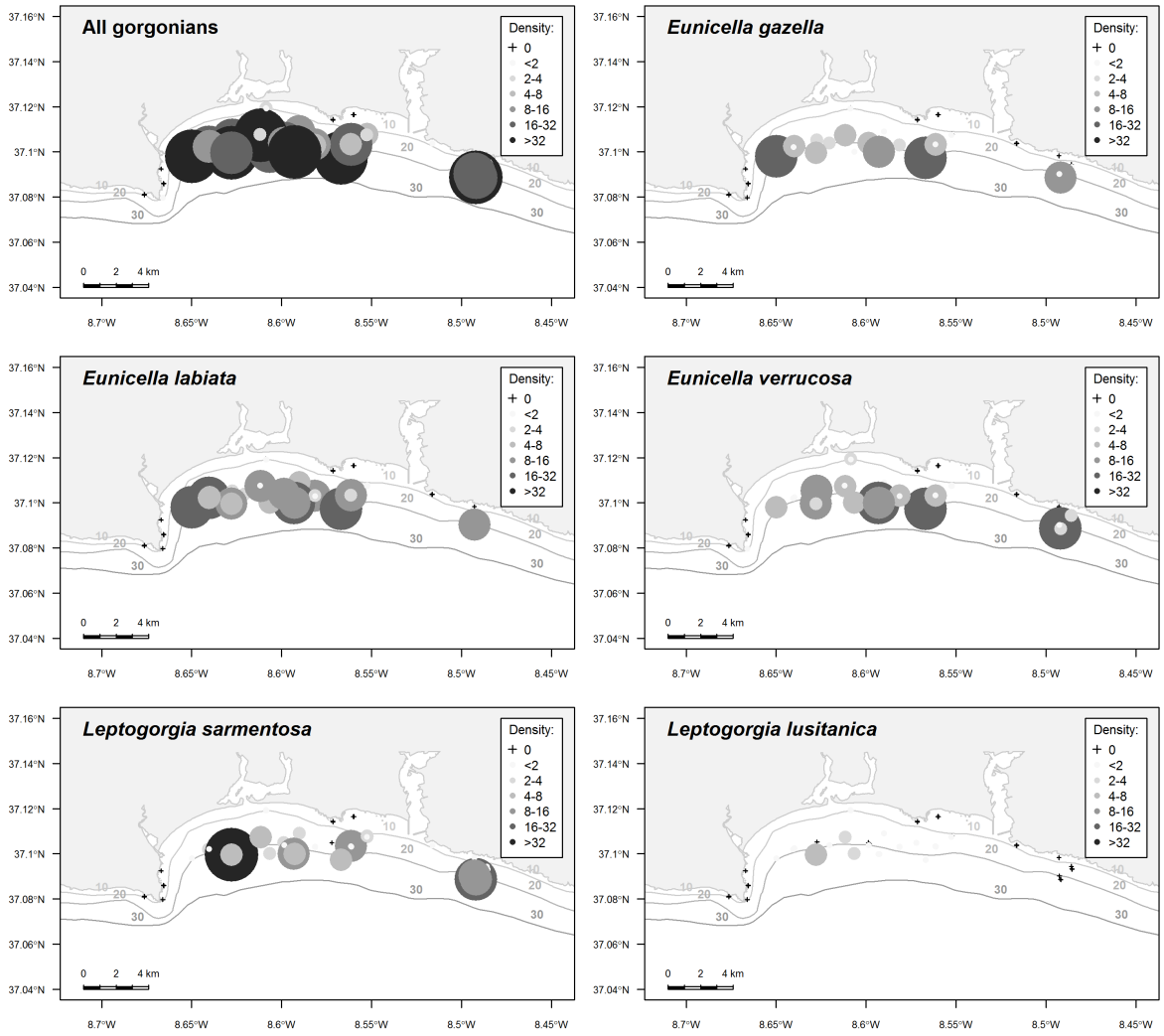

Figure 1.2.: Spatial distribution of gorgonian species in Lagos Bay. The size of the bubbles reflects the abundance of the gorgonians at each transect. Density is presented as number of colonies 5 m^{-2}.

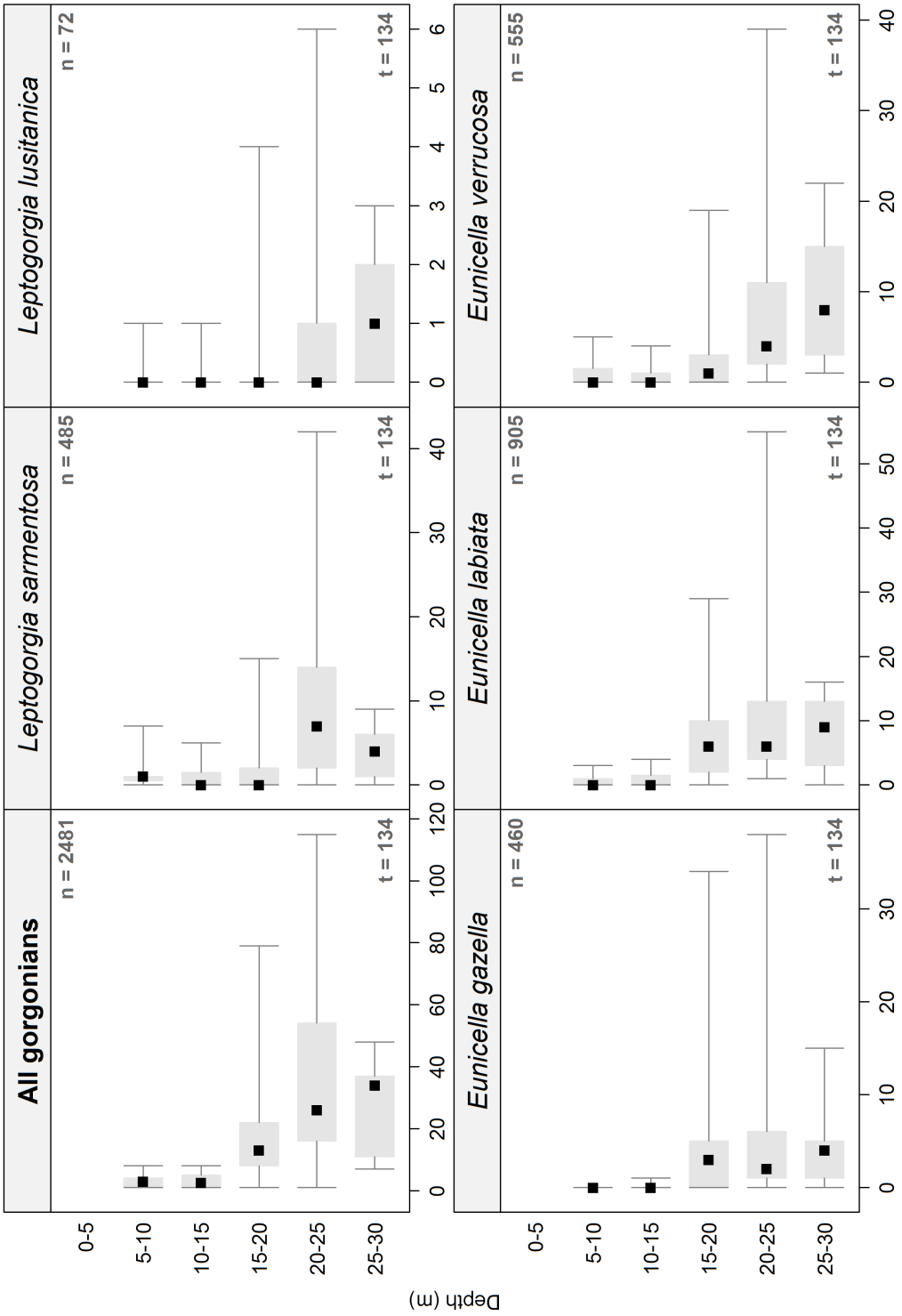

Figure 1.3.: Depth distribution of gorgonian species' abundance in Lagos Bay. Data corresponds to transects grouped into depth levels. The black square represents the median; the box indicates the first and third quartiles; and the line denotes the range. Total number of colonies (n) and samples (t) are indicated for each species.

Table 1.1.: Gorgonian presence and frequency of occurrence at the different depth levels for the whole gorgonian assemblage (All gorgonians) and each species separately. t - number of transects sampled; twg - transects with gorgonians; n - number of colonies.

Depth level	All gorgonians			Species			Colonies		Density		
	t	twg	(%)		twg	(%)	n	(%)	Mean	SE	maximum
0-5	9	0	(0.0)	—	0	(0.0)	0	(0.0)	—	—	—
5-10	63	11	(17.5)	*Eunicella labiata*	4	(6.3)	6	(16.7)	0.1	0.50	3
				Eunicella verrucosa	5	(7.9)	12	(33.3)	0.2	0.75	5
				Leptogorgia lusitanica	2	(3.2)	2	(5.6)	0.0	0.03	1
				Leptogorgia sarmentosa	8	(12.7)	16	(44.4)	0.3	0.76	7
10-15	24	16	(66.7)	*Eunicella gazella*	3	(12.5)	3	(6.1)	0.1	0.00	1
				Eunicella labiata	7	(29.2)	14	(28.6)	0.6	0.44	4
				Eunicella verrucosa	7	(29.2)	12	(24.5)	0.5	0.42	4
				Leptogorgia lusitanica	2	(8.3)	2	(4.1)	0.1	0.13	1
				Leptogorgia sarmentosa	7	(29.2)	18	(36.7)	0.8	0.65	5
15-20	72	69	(95.8)	*Eunicella gazella*	50	(69.4)	260	(24.1)	3.6	0.72	34
				Eunicella labiata	61	(84.7)	484	(44.9)	6.7	0.85	29
				Eunicella sp.	1	(1.4)	1	(0.1)	0.0	—	1
				Eunicella verrucosa	48	(66.7)	181	(16.8)	2.5	0.59	19
				Leptogorgia lusitanica	16	(22.2)	26	(2.4)	0.4	0.23	4
				Leptogorgia sarmentosa	35	(48.6)	125	(11.6)	1.7	0.57	15
20-25	30	29	(96.7)	*Eunicella gazella*	23	(76.7)	153	(14.4)	5.1	1.78	38
				Eunicella labiata	29	(96.7)	327	(30.7)	10.9	2.43	55
				Eunicella verrucosa	26	(86.7)	264	(24.8)	8.8	2.19	39
				Leptogorgia lusitanica	9	(30.0)	30	(2.8)	1.0	0.60	6
				Leptogorgia sarmentosa	24	(80.0)	291	(27.3)	9.7	2.18	42
25-30	9	9	(100.0)	*Eunicella gazella*	7	(77.8)	44	(17.3)	4.9	1.97	15
				Eunicella labiata	8	(88.9)	74	(29.1)	8.2	1.80	16
				Eunicella singularis	1	(11.1)	3	(1.2)	0.3	—	3
				Eunicella verrucosa	9	(100.0)	86	(33.9)	9.6	2.44	22
				Leptogorgia lusitanica	6	(66.7)	12	(4.7)	1.3	0.37	3
				Leptogorgia sarmentosa	8	(88.9)	35	(13.8)	3.9	1.08	9

from 7.5 m, *Eunicella verrucosa* from 8.0 m, *Eunicella labiata* and *Leptogorgia lusitanica* from 8.7 m and *Eunicella gazella* from 11.6 m. The increase of gorgonians' abundance with depth was evident and common to the most frequent and abundant species (Figure 1.3). Up to 15 m, gorgonians were rare or presented very low abundance. At depths deeper than 15 m all species increased in abundance and showed similar trends. At 20–25 m, more than 5 colonies m^{-2} were found in Lagos Bay. All species showed large variation in abundance at 15–20 m and 20–25 m, especially the most abundant and frequent ones (Figure 1.3).

Significant differences were found in the abundance of all species at different depth levels (Table 1.2). For the most abundant and frequent species, *Eunicella labiata*, significant differences were found between depth levels below and above 15 m (Table 1.2). The second most abundant species, *Eunicella verrucosa*, showed significant differences between 10–15 m and 20–25 m,

Table 1.2.: Results of Kruskal-Wallis' U test (*H*) for the abundance of gorgonians at each depth level. Results of the multi-comparison tests using Berhens-Fisher are also given. NS - not significant; * - P<0.05; ** - p<0.01; *** - p<0.001.

Species	*H*	P		Behrens-Fisher test			
All gorgonians	46.30	<0.001		5-10	10-15	15-20	20-25
			5-10		*	***	***
			10-15			***	***
			15-20				NS
			20-25				
Eunicella gazella	37.45	<0.001		5-10	10-15	15-20	20-25
			5-10		NS	***	**
			10-15			***	*
			15-20				NS
			20-25				
Eunicella labiata	46.57	<0.001		5-10	10-15	15-20	20-25
			5-10		*	***	***
			10-15			***	***
			15-20				NS
			20-25				
Eunicella verrucosa	36.44	<0.001		5-10	10-15	15-20	20-25
			5-10		NS	***	***
			10-15			*	***
			15-20				NS
			20-25				
Leptogorgia lusitanica	11.16	0.0109		5-10	10-15	15-20	20-25
			5-10		NS	**	NS
			10-15			NS	NS
			15-20				NS
			20-25				
Leptogorgia sarmentosa	22.72	<0.001		5-10	10-15	15-20	20-25
			5-10		NS	***	**
			10-15			NS	*
			15-20				NS
			20-25				

whereas *Leptogorgia sarmentosa* showed differences between 20–25 m (its highest abundance) and the shallower depth levels (up to 15 m). *Eunicella gazella* was absent above 10 m and rare at 10–15 m, increasing significantly its abundance with depth. *Leptogorgia lusitanica* exhibited low abundance but still the same increasing pattern with depth. Its abundance was significantly higher at depths below 15 m, even though apparently decreasing at 25–30 m.

An exponential trend was detected between depth and gorgonian's abundance for the bathymetric range of this study (Figure 1.4). All regressions were highly significant (p<0.001) and presented high coefficients of determination (r^2 = 0.438–0.787, except for *Leptogorgia lusitanica* with 0.221). The increase of 1 m in depth is associated with a 10.3–11.0 % increase in the number of colonies of *Leptogorgia sarmentosa, Eunicella gazella* and *Eunicella verrucosa*, with *Eunicella*

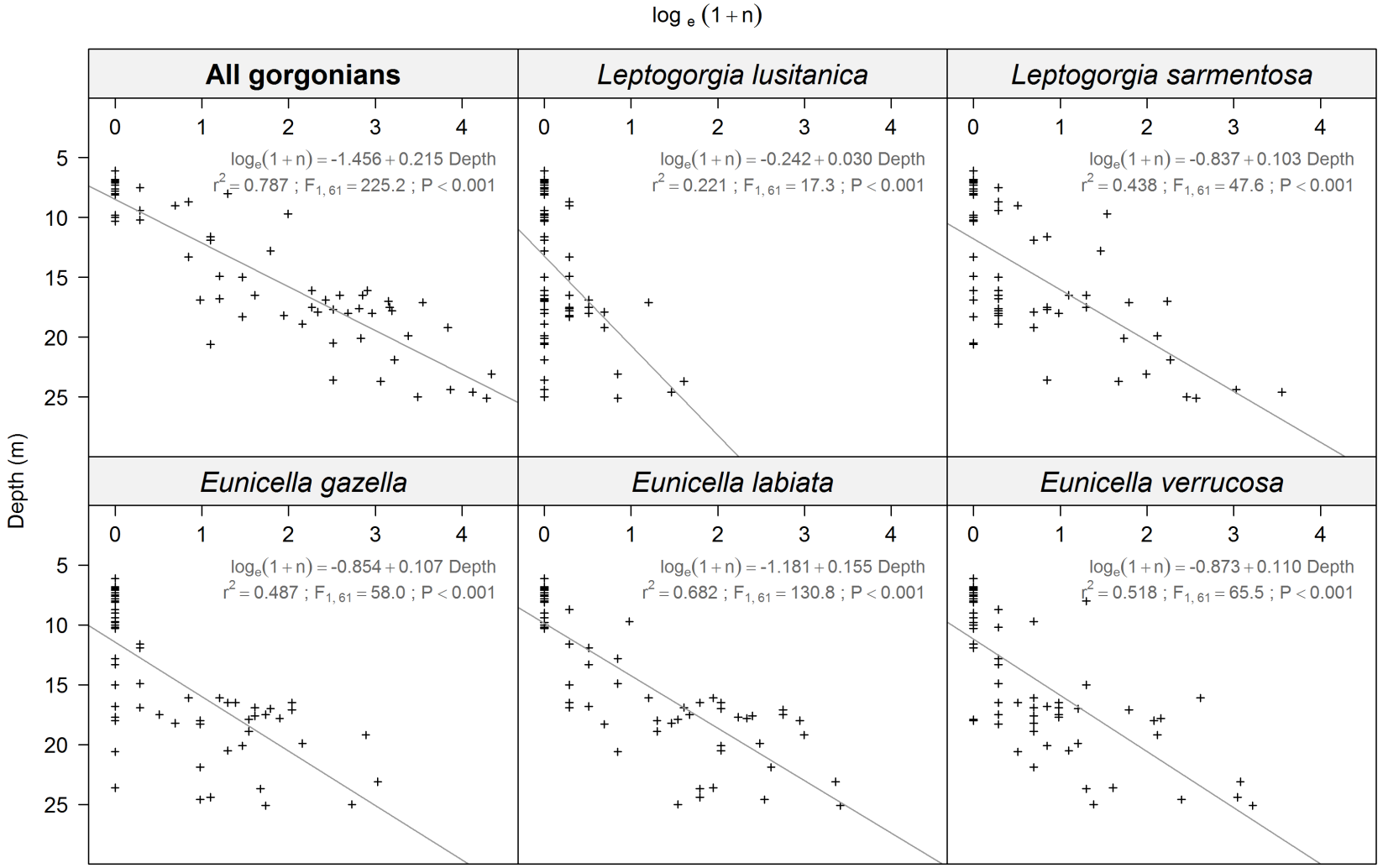

Figure 1.4.: Relationship between depth and abundance of gorgonians in Lagos Bay. The regression equation is presented for each species. The axes of the graphs were rotated for improving the visualization of the depth gradient.

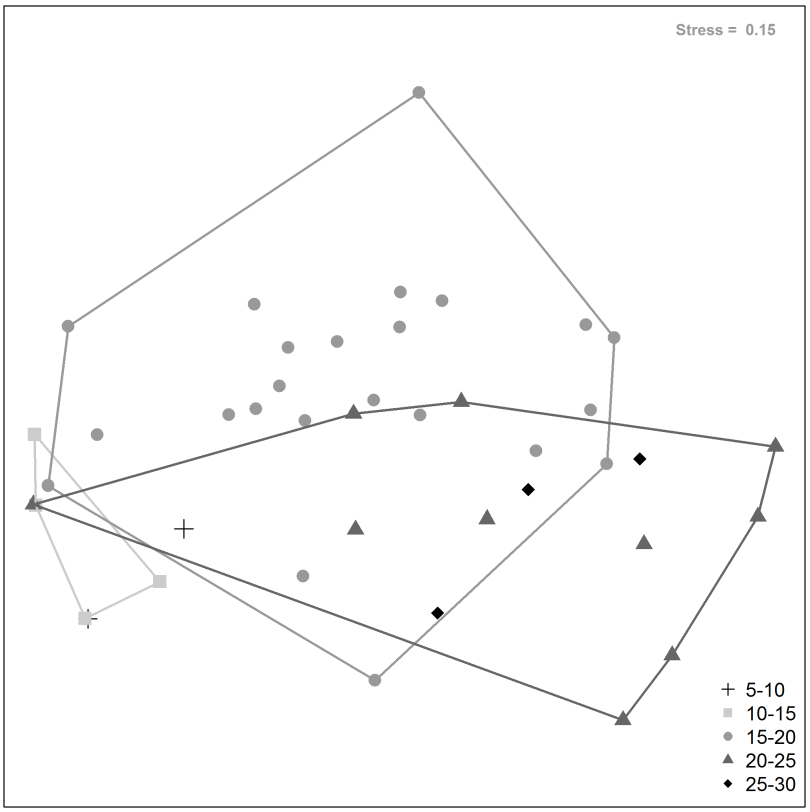

Figure 1.5.: Non-metric multidimensional scaling plot of the gorgonian assemblage data from Lagos Bay (modified Gower index of dissimilarity using $\log_2(x+1)$ transformed data).

labiata showing the highest percentage (15.5 %) and *Leptogorgia lusitanica* presenting a much lower value (3.0 %). The rates of increase in the two latter species were significantly different from the remaining (*Leptogorgia lusitanica*, ANCOVA, p<0.001; *Eunicella labiata*, ANCOVA, p<0.05).

The non-metric multidimensional scaling diagram (Figure 1.5) shows a depth gradient from left to right, reflecting differences in abundance within each depth level. The composition and structure of the gorgonian assemblages in Lagos Bay presented significant differences (Permanova, Pseudo F = 4.07, $p < 0.001$), due to higher abundances at deeper sites. However, the generally low indicator values (IndVal 0.31–0.44; $p > 0.05$) showed that the composition of the assemblages was similar at all depth levels and most species (except *Eunicella singularis*) occurred in several depth levels. The assemblage was characterized by a dynamic alternation in species rankings with *Eunicella labiata* being in the top two ranks along the studied depth range and *Leptogorgia sarmentosa* alternating from first to fourth in rank. The low abundance of *Leptogorgia lusitanica* was reflected in its rank position, fifth at all depth levels.

Four species were highly associated, coexisting in a large number of the samples. *Eunicella labiata*, *Eunicella verrucosa*, *Eunicella gazella* and *Leptogorgia sarmentosa* presented high values

of the three indices used (Ochiai, 0.68–0.85; Dice, 0.68–0.84; Jaccard, 0.51–0.74, all indices range from 0–1), whereas *Leptogorgia lusitanica* showed lower values (Ochiai, 0.46–0.58; Dice, 0.38–0.50; Jaccard, 0.24–0.33) and *Eunicella singularis* presented extremely low levels of association with the remaining gorgonian species (0–0.19).

1.3.2. Relationship between gorgonians and potential competitors

The distribution of erect algae (mainly Chlorophyta and Phaeophyta) and Porifera in Lagos Bay is also depth-dependent. The abundance of erect algae (dominated by *Dictyota dichotoma*, *Asparagopsis armata*, *Halopteris filicina*, *Gelidium latifolium* and *Peyssonnelia rubra*) declined along the depth gradient. In the other hand, the Porifera clearly increased their abundance with depth (Figure 1.6). This group was dominated by encrusting forms such as *Phorbas fictitius*, *Scopalina lophyropoda*, *Cliona viridis*, *Axinella damicornis* and *Chondrosia reniformis* and massive erect forms such as *Crella elegans* and *Axinella polypoides*. A significant negative correlation (Linear regression, $r^2 = 0.439$, $F_{1,11} = 8.605$, $p < 0.05$) between the percentage cover of erect algae and the number of gorgonian colonies was found in Lagos Bay, whereas a positive correlation (Linear regression, $r^2 = 0.769$, $F_{1,11} = 36.67$, $p < 0.05$) was detected between sponges and gorgonians (Figure 1.6).

1.4. Discussion

According to Weinberg (1978), the two main factors affecting the octocorallia communities are irradiance and presence of sediment in the substrate. The amount of light reaching an underwater surface is related to depth, even though it depends on several factors, namely transparency and suspended particles (Gili et al., 1989). Depth, slope and the interaction of these two factors have been reported as presenting a marked positive effect in Anthozoa species distribution (Gili et al., 1989). Indeed, many studies highlighted major variations of physical (e.g. currents, sedimentation) and chemical variables (organic matter content) along the depth gradient, with consequences for the distribution of marine communities (e.g. Garrabou et al., 2002; McArthur et al., 2010).

The present study detected a clear depth pattern in the distribution of all gorgonian species in Lagos Bay, suggesting that the ecology of these suspension feeders is strongly affected by environmental factors that may change with depth and their interactions, such as currents, sedimentation and organic matter. For most species, the general pattern found indicated increasing abundances with depth within the analysed depth range. The present study also revealed that the 15 m bathymetric seems to be an important turning point in the distribution of most gorgonian species in Lagos Bay, which can be related to higher irradiance above this depth but also to higher surf

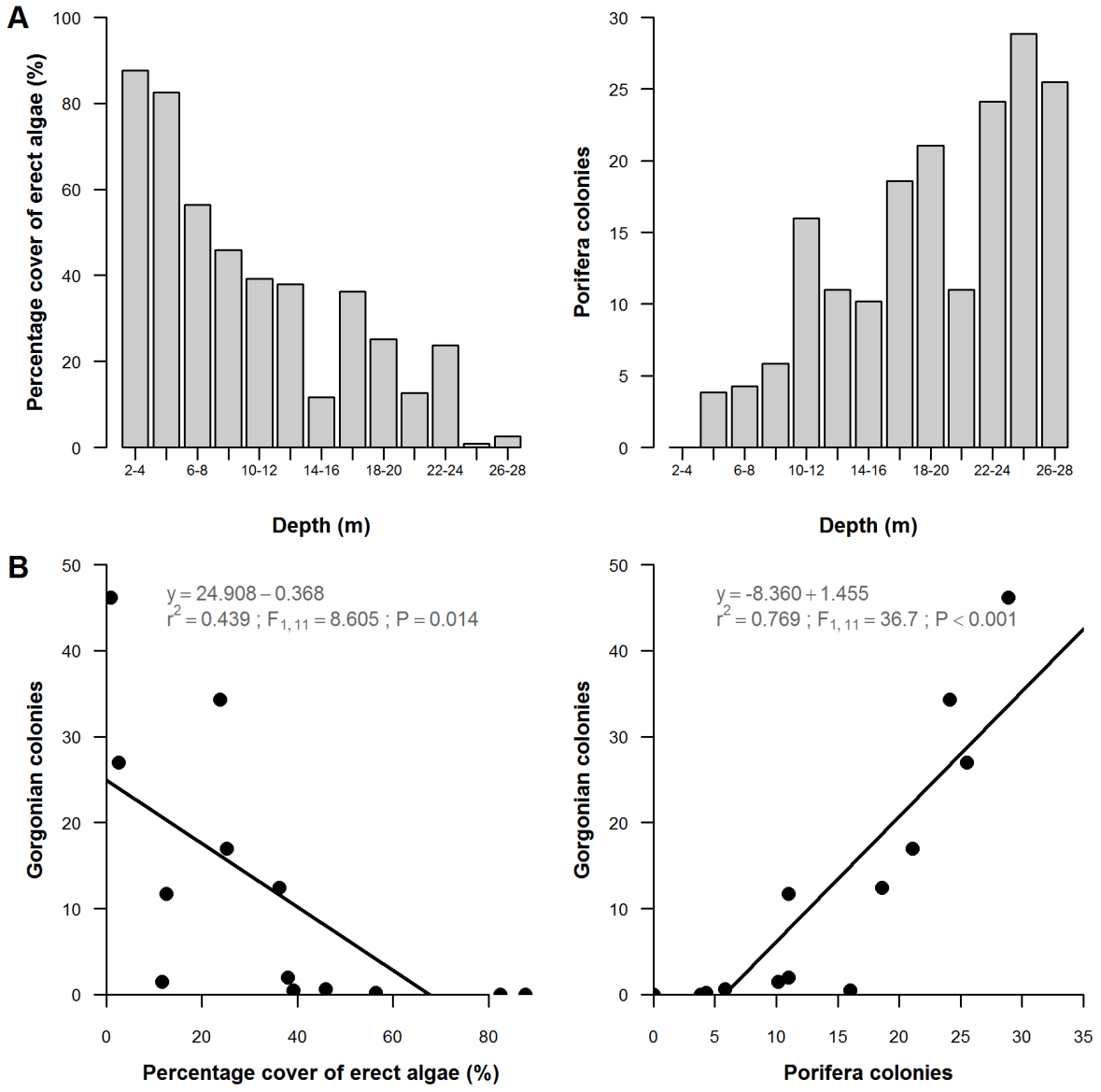

Figure 1.6.: Percentage cover of erect algae and abundance of Porifera along the depth gradient (A) and linear regressions between these faunal groups and the number of gorgonian colonies in Lagos Bay (B).

impact. Indeed, in the Algarve, the lower beach profile limit (closure depth), where wave action is able to disturb the sea bottom, is around 10 m below mean sea level (Dolbeth et al., 2007; Almeida et al., 2011), which is known to influence the patterns of benthic communities (Dolbeth et al., 2007; Carvalho et al., in press). The upper depth distribution limit of the dominant gorgonians in Lagos Bay was very similar suggesting that they are determined by abiotic conditions as observed elsewhere (Zabala and Ballesteros, 1989; Linares et al., 2008a), especially the high water motion of shallower coastal areas. The combination of both factors (strong irradiance and surf) was already reported as being determinant in the distribution of western Mediterranean gorgonian species (Weinberg, 1978). Depth distribution in tropical shallow water gorgonians is also mainly governed by light (Sánchez et al., 1998) and other environmental factors affecting light (e.g. bed load, Yoshioka and Yoshioka, 1989), mainly because most species are zooxanthellate (Dahlgren, 1989; Sánchez et al., 1998). In opposition, shallow water gorgonian assemblages in the Algarve are dominated by azooxanthelate octocorals, and the zooxanthelate gorgonian *Eunicella singularis* is rarely sampled (and the presence of zooxanthelae in the few colonies found in the Algarve was not confirmed). Besides, in the present study, erect algae dominated the biocenoses at low depth but rapidly decreased their abundance when light intensity is reduced, with their abundance being inversely correlated to the abundance of gorgonians. In shallow water, algal-dominated benthic communities present species that favour out-competition processes being continuously replaced (Garrabou et al., 2002). In contrast, animal-dominating deeper communities tend to present slow growth species avoiding competition displacement and enhancing the maintenance of diversity and complexity (Garrabou et al., 2002). However, there is a depth range (12–20 m) where the abiotic conditions seem suitable both for erect algae and gorgonians where competition for space occurs, explaining the negative correlation between the two groups. In fact, anthozoans are unable to compete with large algae where light intensity is high (Gili et al., 1989; Zabala and Ballesteros, 1989) supporting the idea that the bathymetric behaviour of gorgonian species in Lagos Bay may be only indirectly linked to light intensity. Therefore, ecological processes, such as competition, rather than physical processes alone may influence the depth distribution of gorgonians in shallower waters. In the Mediterranean, a similar model has been proposed, consisting of three zones: a superficial zone (0–10 m) dominated by erect algae, a mixed zone (10–15 m) co-dominated by erect algae, crustose algae and suspension feeders and a third zone (15–42 m) dominated by suspension feeders (Zabala and Ballesteros, 1989). But in Lagos Bay, competition for space and food was not apparent between gorgonians and sponges. Both groups presented similar distribution patterns with depth and were positively correlated indicating that, if competition is occurring, it is kept at low levels. The habitat requirements of the species that compose these two suspension feeding groups are probably different with small overlap. Massive erect sponges such as *Crella elegans* and *Axinella polypoides* may compete for space with gorgonians, but these are only a part of the Porifera assemblage (percentage cover of sponges was not assessed) dominated by encrusting forms that use the available space below erect forms efficiently. Regarding food

sources, sponges mainly feed on very small particles, such as suspended particles, free-living bacteria and colloidal organic matter, being extremely efficient at capturing particles down to 0.1 µm (Ruppert and Barnes, 1994; Riisgård and Larsen, 2010). On the other hand, gorgonians mainly feed on larger particles such as zooplankton and particulate organic carbon, with some species, such as *Leptogorgia sarmentosa* presenting a wide spectrum of food sources being able to feed on particles as small as 4 µm (Ribes et al., 2003). Considering that, of the species found in Lagos Bay, those with smaller polyps are the *Leptogorgia*, it is not expectable that the feeding habits of the remaining species considerably overlap with particles that can be filtered by sponges, thus allowing us to suggest that competition for food must be relatively low in Lagos Bay and passive (gorgonians) and active (sponges) suspension feeders can co-exist (Gili and Coma, 1998). Concerning competition between gorgonian species, the similarity in depth distribution patterns, and the high association of the most abundant species suggests that these slow-growth species are not competing among themselves. The lower coexistence of *Leptogorgia lusitanica* with the more abundant species may be due to its lower abundance in Lagos Bay being absent in a high number of samples. In fact, the only case of competition between gorgonians reported for nearby areas concerns the mutual exclusion of *Eunicella cavolinii* and *Eunicella verrucosa* in Mediterranean coralligenous habitats (Carpine and Grasshoff, 1975). However, until now, *Eunicella cavolinii* has not been found in the Algarve, and there is no evidence that *Eunicella verrucosa* distribution is being constrained by competition. It is important to notice that the strong associations found between the gorgonian species that are more representative of Lagos Bay should be addressed with care as competition may take place at lower scales (<5 m). At deeper depths, where abiotic factors are more homogeneous, benthic communities are sometimes dominated by suspension feeders and patchy in nature (Zabala and Ballesteros, 1989; Garrabou et al., 2002), with some gorgonian species showing a patchy distribution pattern (Linares et al., 2005). In this context, scale is determinant for niche dynamics in space (Pearman et al., 2007) and the used scale may encompass different niches used contrastingly by species, with insufficient resolution to ascertain differences between gorgonian species.

Concerning the gorgonian assemblage composition, four species are well represented in the area, with *Eunicella labiata* being the most abundant and *Eunicella verrucosa*, *Eunicella gazella* and *Leptogorgia sarmentosa* presenting similar abundance. Of these dominant gorgonians, the *Eunicella* species are poorly represented in the Mediterranean, where shallow water gorgonian assemblages are dominated by *Paramuricea clavata*, *Eunicella singularis* and *Leptogorgia sarmentosa* (e.g. Ballesteros, 2006; Gori et al., 2011a). However, the abundance of each dominant species in the Mediterranean is clearly associated to habitat characteristics such as vertical facies, soft bottoms, maerl, pebbles and rocks (Gori et al., 2011a), suggesting different ecological requirements. On the contrary, in Lagos Bay, the distributions of the dominant gorgonian species were all well correlated (species occurring at the same sites) suggesting that the rocky areas are relatively homogeneous with respect to available niches for several gorgonian species. However,

because the study was restricted to rocky areas, the environmental gradients in several topographic and environmental factors that can affect the distribution of gorgonians are relatively short, minimizing the influence of those factors in the distribution of some species.

The most frequent and abundant species found, *Eunicella labiata*, is relatively common in coralligenous habitats near the Strait of Gibraltar (González, 1993), but to the authors' best knowledge, this species has only been reported recently for the Algarve coast (Gonçalves et al., 2007; Vieira, 2008), probably resulting from erroneous identifications in the past. Another recent study also reported its occurrence in the Professor Luiz Saldanha Marine Park (Arrábida, Center Portugal) (Rodrigues, 2008), where it was frequent but not dominant. Another abundant *Eunicella* species in Lagos Bay, *Eunicella verrucosa* has been described as an Atlantic species with a wide vertical range. In the current study, this species was found from 8 to 27 m, which agrees with data from the Strait of Gibraltar, where it occurs from 6 to 87 m (González, 1993). However, in the Mediterranean this species is only found at deeper waters (35 to 200 m) because of the competition with *Eunicella cavolinii*, which occurs mainly between 10 and 30 m (Carpine and Grasshoff, 1975). The wider bathymetric range observed both in Lagos Bay and the Strait of Gibraltar may be due to the lack of competitive exclusion by *Eunicella cavolinii*, which was not observed in both areas but is common in the Mediterranean. The other species dominating the assemblages in Lagos Bay, *Eunicella gazella*, presented a distribution positively correlated to that of *Eunicella verrucosa*, which once more is in agreement with the findings by González (1993) in the Strait of Gibraltar, where they are also commonly found together.

The dominance of *Leptogorgia sarmentosa* in the study area may be related to the presence of sediment particles in the rocky bottom. Indeed, this species is clearly associated with areas with frequent but moderate disturbance, where sediment re-suspension is high (Gori et al., 2011a), and has been pointed as an indicator of silt (Weinberg, 1978, reported as *Leptogorgia ceratophita*). Although it has been reported to inhabit different substrates, namely rocky areas, shells on biodetritic sediments and sandy muddy areas (González, 1993), it shows a high correlation with soft bottoms or surfaces where sediments tend to accumulate (Gori et al., 2011a). The preferential distribution of *Leptogorgia sarmentosa* within areas of high sedimentation rates may be related to its feeding requirements, as it is known that re-suspended particles are particularly important for this species' diet (Ribes et al., 2003; Rossi et al., 2004). According to our observations, sediment transport (bed load) is high in the Lagos Bay area, probably because this area is near the Rio Arade estuary, Ria de Alvor (coastal lagoon) and Ribeira de Bensafrim (creek). The habitat conditions in Lagos Bay clearly favour this species as the area is mainly characterized by low relief rocky plateaus with a thick layer of fine sediments that are easily re-suspended (submerged rock bottoms). In the Mediterranean, this species is abundant in sheltered areas with turbulent circulation but without strong near-bottom currents (Gori et al., 2011a). Regarding *Leptogorgia lusitanica*, even though its ecological requirements are still poorly understood, it has been described as preferring habitats

with weak to moderate hydrodynamics but clear waters (González, 1993). In fact, in other areas of the Algarve coast where sedimentation and turbidity is lower, this species presents higher abundance at similar depths (e.g. Pedra da Greta and Pedra do Barril, authors' unpublished data).

The low abundance and frequency of occurrence of *Eunicella singularis* was already expected, as it is a Mediterranean species with limited distribution outside this area. This species is one of the dominant taxa in the coralligenous communities in the Mediterranean Sea (Ballesteros, 2006; Gori et al., 2011a) and can be found on horizontal or slightly sloped surfaces in light-rich areas, having a marked dependence on light. Indeed, this is the only gorgonian species in the Mediterranean area presenting zooxanthellae, but has been reported from 6–67 m. The preferential habitat described for this species is frequent in the study area, but the species was rarely found in Lagos Bay. We hypothesize that the colonies found in the study area are colonizers from Mediterranean populations that under favourable conditions were able to reach and settle in suitable rocky areas of the Algarve coast.

Final remarks

The present study provides invaluable information on the spatial and depth distribution of gorgonian species in shallow rocky bottoms near the westernmost part of continental Europe. The key role of gorgonians in the infralittoral rocky communities poses another challenge, the capacity of these animals to cope with both thermal stress but also pathogens under a climate change scenario, an important issue for the future management of coastal marine ecosystems. The present data is also relevant for the establishment and management of future MPAs in southern Portugal, a common management tool in several areas of the world, namely in the Mediterranean, where gorgonians are used as ecological indicators. What is more, "coral gardens", including gorgonian dominated biocenoses in south Portugal and Spain have been recently proposed for the OSPAR (Convention for the Protection of the marine Environment of the North-East Atlantic) list of protected habitats (Anonymous, 2011). Therefore, reference data like the one provided by this study may be relevant for future monitoring programmes. In Lagos Bay, the abundance of all gorgonian species increases with depth, showing a strong association to another suspension feeding benthic taxa, the Porifera. The specific ecological requirements regarding space and food of the two taxonomical groups probably present low overlap, thus competition levels shall be low. However, at shallower depths, gorgonians seem to be out-competed by algae for space, even though the upper limit in the distribution of gorgonians in Lagos Bay is probably mostly related to abiotic factors such as high water movement. Further multidisciplinary studies, with broader spatial and temporal scales but also wider depth ranges, supported by modern technology (e.g. ROVs and remote sensors) should be undertaken in order to elucidate on the abiotic and biotic factors that might be affecting the distribution of these octocorals in the Algarve coast.

Acknowledgements

J.C. (SFRH/BD/29491/2006) benefits from a PhD grant awarded by “Fundação para a Ciência e a Tecnologia” (FCT)’. This study was performed in the framework of the research project Rensub (http://www.rensub.com), funded by ARH Algarve and POVT.

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CHAPTER 2

Indirect evidence of human pressure on the spatial distribution and size structure of gorgonian populations in the south of Portugal

Submitted to: *Biodiversity and Conservation*

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Abstract

The gorgonian fauna of the southern Portuguese coast is composed by species of different origins: NE Atlantic (*Eunicella verrucosa*, *Leptogorgia lusitanica*), Mediterranean (*Leptogorgia sarmentosa*, *Eunicella singularis*, *Paramuricea clavata*) and North Africa (*Eunicella labiata*, *Eunicella gazella*), highlighting the importance of this geographical area for the fluxes of biological diversity. While the western Mediterranean assemblages are mainly monospecific, in the south coast of Portugal, there is a high association of several gorgonian species that co-dominate assemblages even though differing in structure. The analyses of size-frequency distributions and abundance suggest that the spatial patterns of gorgonian distribution along the southern coast of Portugal are driven by the interaction of both natural and anthropogenic pressures. Although larger colonies were not restricted to the sites with lower fishing pressure, gorgonian populations sampled in more intensively fished areas generally presented skewed distributions towards small sizes, and more peaked than normal distributions. The effects of natural disturbance events on the structure of gorgonian populations were evidenced by distinct demographic patterns in nearby areas under similar anthropogenic pressure. The existence of a thick sediment layer over the hard bottoms in the disturbed area suggests that sedimentation may have caused a high mortality in small sized gorgonians and prevented the settlement and/or recruitment, resulting in a bimodal distribution. This study also provides evidence that the response of gorgonians to disturbance is species-dependent: *Eunicella labiata* does not seem to be affected; *Leptogorgia sarmentosa* seems to be affected mainly by anthropogenic pressures; *Eunicella gazella* and *Leptogorgia lusitanica* seem to be affected by both kinds of stress.

Keywords: shallow water gorgonians • *Leptogorgia* • *Eunicella* • spatial distribution • size-frequency distribution • species coexistence • disturbance • fisheries

2.1. Introduction

Gorgonians are colonial organisms with a relevant role in the marine ecosystem namely by stabilising soft-substrata, enhancing sedimentation and promoting the increase of local biodiversity (Bruno and Kennedy, 2000; Cerrano et al., 2009). Nevertheless, over the last decades, several studies reported that gorgonians are severely affected either by anthropogenic pressure, such as fishing (Bavestrello et al., 1997; Willison et al., 2000; Chiappone et al., 2002, 2005), anchoring, scuba diving (Coma et al., 2004; Linares et al., 2008d; Di Franco et al., 2009) and pollution (Bruno et al., 2003; Cerrano and Bavestrello, 2008), or natural disturbances (Martin et al., 2002; Linares et al., 2005; Coma et al., 2006; Burkepile and Hay, 2007; Schiaparelli et al., 2007; Garrabou et al., 2009;

García-Matucheski and Muniain, 2010; Huete-Stauffer et al., 2011). Anthropogenic pressures are known to cause partial or total mortality of the gorgonian colonies, reduction in competitive ability, higher risk of disease, and lower growth rates, fertility and reproductive capacity (e.g. Weinberg, 1978; Coma et al., 2004; Linares et al., 2008c). Besides, the effects of human activities are known to be size-dependent (Shin et al., 2005; Jennings and Reynolds, 2007). Body size of a species is crucial for its ecology, life history, population dynamics, and exploitation vulnerability, since it is related to life history traits such as somatic growth rate, fecundity and age at maturity (Reynolds et al., 2001), namely in scleractinian corals (Meesters et al., 2001) and octocorals (Yoshioka, 1994; Coma et al., 1995; Tsounis et al., 2006; Linares et al., 2007). Consequently, size-frequency distributions of marine species have been used for environmental impact assessment (Shin et al., 2005).

In the past few years, management plans focusing on the whole ecosystem have been advocated [Ecosystem Based Management (McLeod et al., 2005) and Ecosystem Approaches to Management (Murawski, 2007)], and the need for data on ecosystem structure, namely at the population level has been emphasized (e.g. Levin and Lubchenco, 2008; Ellis et al., 2011). Particularly in the Mediterranean, several studies have been undertaken in order to gather a large set of biological and ecological information regarding gorgonian fauna (Linares et al., 2007, 2008d; Bramanti et al., 2009). Indeed, information on spatial distribution patterns, growth, reproduction and dispersion is crucial to build up predictive models to be used in conservation plans (Benedetti-Cecchi et al., 2003; García-Charton et al., 2008; Costello et al., 2010). In contrast, information concerning spatial distribution and ecological requirements of shallow water gorgonians in the NE Atlantic is scarce, namely in the south coast of Portugal. Because of its geographic location, this area harbours a rich marine fauna with biogeographic affinities to the Temperate Northern Atlantic (Mediterranean Sea, Lusitanian and Northern European Seas provinces) and Tropical Atlantic (the west African Transition, and Northwestern/Southwestern Atlantic provinces) (sensu Spalding et al., 2007; Souto et al., 2010; Levy et al., 2011), because of the proximity to the Strait of Gibraltar (Baus et al., 2005, and references therein) and the confluence of different oceanic currents (Cherubin et al., 2000; Pérez et al., 2001; Coelho et al., 2002; Martins et al., 2002). As such, it is expected that this area presents particular features in what concerns the composition and structure of gorgonian fauna. Besides, information on such a particular geographic area can also be crucial for a better knowledge on the patterns and processes underlying the overall distribution of gorgonians in Atlantic and Mediterranean waters.

To overcome the lack of information on the occurrence and abundance distribution patterns of gorgonian species of shallow rocky habitats, several transects were established along the southern coast of Portugal. Because previous studies showed that gorgonian populations may be affected by anthropogenic activities, sampling comprised areas under different levels of human pressure. Therefore, the present study aims at contributing for an insight knowledge on shallow water gorgonians in the NE Atlantic rocky habitats and to assess potential effects of anthropogenic

activities on such populations. Specifically, the following questions will be addressed: i) what are the main distribution patterns of gorgonians along the southern coast of Portugal?; ii) are there differences in structure and composition of the assemblages under different intensity of human pressure?; iii) can size-frequency distributions of dominant species be used as a proxy to assess the vulnerability of the assemblages?

2.2. Materials and Methods

2.2.1. Study area

This study was conducted in the south coast of Portugal (Algarve), characterized by heterogeneous coastline and sublittoral areas. In general, the circulation patterns in the Iberian Peninsula are dominated by seasonal upwelling (spring-summer) and downwelling (winter) events associated to northerly and southerly winds, coupled to the North Atlantic Oscillation (Sánchez et al., 2007). The coastal flow along the SW Iberian Peninsula has an alternating nature, featuring sharp current inversions on time scales of less than two days (Relvas et al., 2007), with a dominant alongshore flow on the inner shelf of the northern margin of the Gulf of Cádiz (Sánchez et al., 2006). Topographic features such as the submarine canyon of Portimão and the Cape São Vicente interact with the Mediterranean Outflow Water forming eddies that characterize the circulation patterns at the mesoscale (Cherubin et al., 2000). Salinity is fairly constant 35.0–36.0 but sea surface temperature presents a marked seasonal variation between 14 and 24 °C depending on whether upwelling or downwelling dominates.

The western part of the Algarve coast (Barlavento) is generally characterized by rocky formations of several types (e.g. underwater spurs, boulders, low relief rocky areas, submerged rock bottoms), by different sediment dynamics, and also different human activities over the entire area. The coastal area near Lagos (see Figure 2.1), in particular, is morphologically complex, presenting rocky areas with cliffs forming small beaches, a large bay with extensive sandy beaches and dunes, a coastal lagoon (Ria de Alvor) and the Arade and Bensafrim estuaries. The shallow continental shelf (down to ≈30 m depth) is generally characterized by rocky outcrops with pockets of rubble and/or sand. In the eastern part of the Algarve coast (Sotavento), rocky bottoms are scarce and only two large areas are found, Pedra da Greta and Pedra do Barril (Figure 2.1). Apart from these two areas, only small rocky reefs can be found scattered over the large, low relief sandy areas.

Three rocky areas in the Algarve were surveyed. The Lagos Bay is located in the western part of the Algarve that extends from Lagos to Portimão and comprises an area with 20.6 km^2 of rocky bottoms and covers ≈25 km of the Algarve coast with depth ranging from 0 to 30 m. Pedra da Greta

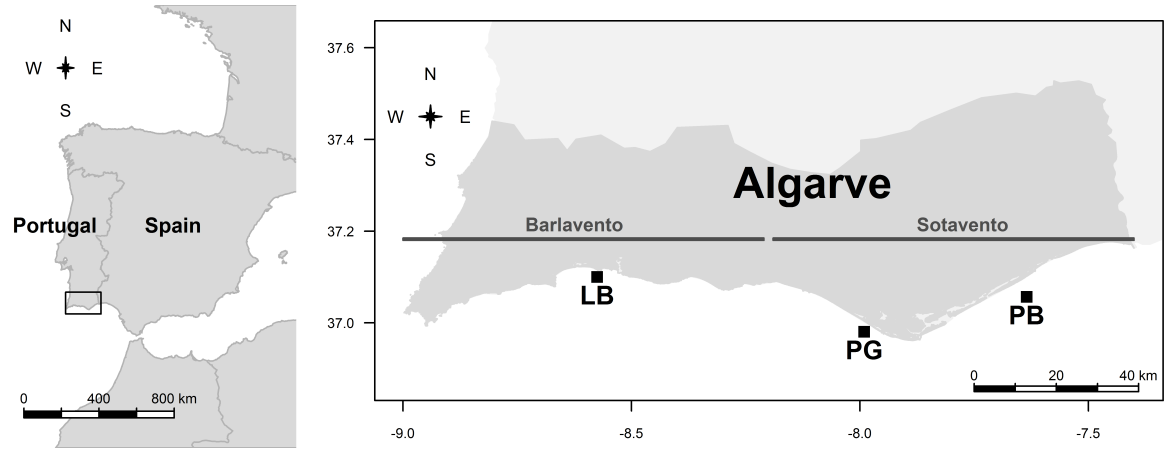

Figure 2.1.: Map of the Algarve with the three study areas: LB - Lagos Bay; PG - Pedra da Greta and PB - Pedra do Barril.

is a rocky outcrop running parallel to the shoreline at 15–18 m depth with ≈2 km length, 50–100 m width and 1–3.5 m height. Pedra do Barril is also a rocky outcrop running parallel to the shoreline at 22–27 m depth with ≈3 km length, 100–150 m width and 2–5 m height. Because the depth range of rocky habitats at Pedra da Greta and Pedra do Barril do not overlap and are more restricted than the rocky habitats at Lagos Bay, in the latter location sampling was stratified by dividing the area into comparable depth ranges (Lagos shallow, 15–20 m; Lagos deep, 20–25 m) to enable proper comparisons.

Some environmental features of the sampled areas are summarized in Table 2.1. Semi-quantitative criteria were set for different environmental parameters (complexity, sediment covering the rocky surfaces, intensity and frequency of underwater currents, re-suspension of sediments) to characterize the different study locations. The sediment type surrounding each area was obtained using sediment classification cartography (Anonymous, 2006a) and the percentage of fine particles (<63 µm) in their vicinity was estimated for a circular area of 4 km diameter using GIS. Generally, Pedra da Greta and Pedra do Barril present higher relief and topographic complexity than Lagos Bay (Table 2.1). The shallower sites, Lagos shallow and Pedra da Greta, are surrounded mainly by medium to coarse sandy sediments whereas Lagos deep and Pedra do Barril neighbour sediment areas characterized by fine particles (<63 µm). Therefore, re-suspension of sediment particles is more likely to occur at the deeper areas resulting in higher proportions of the substrate covered by sediments and lower visibility. In Pedra do Barril, moderate underwater currents re-suspending sediment were frequently observed during sampling.

2.2.2. Human impacts potentially affecting gorgonians in South Portugal

In south Portugal, contamination is largely due to coastal development and industry that

operates in the area, being concentrated in urban areas and influenced by freshwater inputs (Machado et al., 1999; Wayland et al., 2008). Scuba diving has been growing in the past few years and, generally, the western part of the Algarve (Barlavento) presents higher number of divers, dives and diving companies than the eastern part (Sotavento) (IPIMAR unpublished data). However, the number of visits per site is similar at both areas because there are more rocky areas and consequently more diving spots in Barlavento. Moreover, the number of diving companies, divers and dives (IPIMAR unpublished data) are low when compared to those of other areas with intensive scuba diving (e.g. Red Sea, Mediterranean Sea) and the estimates of damage inflicted to gorgonians by scuba divers is low (unpublished data). On the other hand, large storm events are rare, not long-lasting, and of similar intensity across the overall coastal area, and mass mortality events, reported elsewhere (Martin et al., 2002; Linares et al., 2005; Coma et al., 2006; Schiaparelli et al., 2007; Garrabou et al., 2009), have never been reported for the Algarve. Nevertheless, in years of long summer periods of high temperature and calm sea (such as the summers of 2006, 2009, 2010 and 2011, http://www.hidrografico.pt/boias-ondografo.php), there was some evidence of mats covering uniformly the sea bottom rapidly disappearing when water temperature drops and sea roughness increases (JC, personal observation). Therefore, because of the low intensity of the previous potential damaging factors to gorgonians in south Portugal, the most plausible impacts affecting these assemblages seem to be fishing and anchoring that are known to cause complete or partial mortality by physical contact (Bavestrello et al., 1997; Eno et al., 2001; Johnson, 2002; Milazzo et al., 2002). As no spatial data on the distribution of anchoring is available, and there are no major reasons to suspect that anchoring is higher in any of the areas, we accept the hypothesis that this pressure is similar along the coast.

Fishing gears such as seize nets, trammel nets, gillnets, longlines and traps are intensively used by fishermen in the area, being frequently lost along the Algarve coast (Erzini et al., 1997; Santos et al., 2003a,b; Erzini et al., 2008). Due to the scale and importance of commercial fishing in the Algarve, this activity arises as the most important and frequent source of damage for gorgonians, even though very difficult to quantify. It is, however, known that in the Algarve, gorgonians are commonly caught accidentally by fishermen while retrieving fishing gears (Nobre, 1931; Gonçalves et al., 2008; Vieira, 2008).

Some statistics concerning fishing are summarized in Table 2.2, comparing the western (Barlavento; Lagos Bay) and eastern (Sotavento; Pedra da Greta and Pedra do Barril) parts of the coast. The local fleet (vessels with less than 9 m) and the coastal fleet (vessels with more than 9 m) are allowed to fish in the studied areas in shallow waters (Erzini et al., 1997; Santos et al., 2003a; Erzini et al., 2008). Generally, the number of fishing licenses, number of fishing vessels and captures are higher in Sotavento than in Barlavento suggesting a higher fishing effort in the former area. What is more, the area of rocky bottoms in the Sotavento is much lower than in Barlavento, contributing to the concentration of fishing, thus increasing fishing pressure.

Table 2.1.: Environmental characterization of the sampled areas. See the text for details on the presented scales.

	Lagos shallow	Lagos deep	Pedra da Greta	Pedra do Barril	Criteria/Source
Depth	16 m	28 m	15-18 m	22-27 m	
Complexity	1-2	0-1	4	3	adapted from Wilson et al., 2007 [a]
Sediments covering rocky areas	1	4	1	3	percentage of rocky surface covered by sediment [b]
Frequency of underwater currents	0-1	0-1	2	3	percentage of the dives [c]
Intensity of underwater currents	0-1	0-1	2-3	2-3	estimated underwater current speed[d]
Sediment type surrounding areas	Medium Coarse	Fine particles (<63 µm)	Medium Coarse	Fine particles (<63 µm)	Sediment chart (Anonymous, 2006a)
Fine particles in surrounding areas	14.4	66.4	0.0	25.6	percentage (GIS) [e]
Re-suspension of sediments	1	4	2	3	frequency [f]
Visibility	3	1-2	3	1-2	maximum visible range [g]

[a] 0 – no vertical relief; 1 – low and sparse relief; 2 – low but widespread relief; 3 – moderately complex, with rocks and/ or boulders of several sizes; 4 – very complex with numerous fissures and caves; 5 - exceptionally complex with numerous caves, overhangs and canyons.
[b] 0 – 0–20 %; 1 – 20–40 %; 2 – 40–60 %; 3 – 60–80 %; 4 – 80–100 %
[c] 0 – 0 %; 1 – 0–20 %; 2 – 20–40 %; 3 – 40–60 %; 4 – >60 %
[d] 0 –<0.2 m s^{-1}; 1 – 0.2–0.5 m s^{-1}; 2 – 0.5–1 m s^{-1}; 3 – 1–1.5 m s^{-1};4 – >1.5 m s^{-1}
[e] percentage of fine particles (<63 µm) in a circular area (radius of 2 km) around the site. Areas estimated using GIS.
[f] 0 – never; 1 – rarely; 2 – sometimes; 3 – often; 4 – very often
[g] 0 – <0.5 m; 1 – 0.5–2 m; 2 – 2–5 m; 3 – 5–10 m; 4 – >10 m

Table 2.2.: Fisheries information used to estimate fishing pressure on the western (Barlavento) and eastern (Sotavento) parts of the Algarve, namely fleet, captures, and lost fishing gear. Numbers in bold represent the largest numbers. [a] – fish species caught in shallow waters only (<50 m); [b] – octopus and cuttlefish. See source references for details on estimates.

		Barlavento	Sotavento	Source
Fishing effort				
Local (<9 m)	Number of licenses (2010)	2324	**3317**	DGRM, 2011
	Number of boats (2010)	561	**737**	DGRM, 2011
Coastal (>9 m)	Number of licenses (2010)	333	**709**	DGRM, 2011
	Number of boats (2010)	88	**223**	DGRM, 2011
Captures (Ton)	Fish 2006-2010[a]	7606	**8287**	INE, 2011
	Fish 2001-2005[a]	9097	**9703**	INE, 2011
	Molluscs 2006-2010[b]	6591	**15651**	INE, 2011
	Molluscs 2001-2005[b]	8676	**12800**	INE, 2011
Lost fishing gears				
Nets				
Local (<9m)	Number of licences	350	**667**	DGPA, 2001
	Number of vessels using nets	196	**399**	DGPA, 2001
	Mean number of lost nets per vessel	**4.8**	3.2	Santos et al., 2003a
	Estimated number of lost nets per year	940.8	**1276.8**	Santos et al., 2003a
Coastal (>9m)	Number of licences	160	**172**	DGPA, 2001
	Number of vessels using nets	70	**94**	DGPA, 2001
	Mean number of lost nets per vessel	**4.7**	2.8	Santos et al., 2003a
	Estimated number of lost nets per year	**329**	263.2	Santos et al., 2003a
Octopus traps				
Local (<9m)	Number of licences	**190**	103	Erzini et al., 2008
	Number of vessels	**161**	87	Erzini et al., 2008
	Traps per vessel	270.3	**644.4**	Erzini et al., 2008
	Estimated number of traps used	43518	**56063**	Erzini et al., 2008
	Proportion of lost traps	0.11	**0.23**	Erzini et al., 2008
	Estimated number of traps lost per year	4975	**12667**	Erzini et al., 2008
Coastal (>9m)	Number of licences	58	**91**	Erzini et al., 2008
	Number of vessels	49	**77**	Erzini et al., 2008
	Traps per vessel	**995**	903.8	Erzini et al., 2008
	Estimated number of traps used	48755	**69593**	Erzini et al., 2008
	Proportion of lost traps	0.21	**0.35**	Erzini et al., 2008
	Estimated number of traps lost per year	24525	**52604**	Erzini et al., 2008

The information on lost fishing gears by the local fleet operating in shallow waters at both areas reinforces this idea (Table 2.2). Another indicator that fishing pressure in nearshore waters is higher in Sotavento is the number of octopus traps used per vessel by the local fleet and the higher proportions of lost traps for both fleets. Based on this information and also on surface (e.g. number of buoys and fishing vessels) and underwater observations by the authors during the sampling surveys (e.g. lost fishing gears), fishing pressure is higher in Pedra da Greta and Pedra do Barril (Sotavento) than in Lagos Bay (Barlavento) (Table 2.2).

2.2.3. Distribution of gorgonians at the regional scale of the Algarve

The distribution of gorgonians was quantified by means of underwater transects by scuba diving (5 × 1 m belt transects). Specifically, 72 transects were conducted at Lagos shallow and 30 transects at Lagos deep. A total of 20 transects were conducted in Pedra da Greta and 12 in Pedra do Barril. Identification of gorgonian species was based on the studies by Carpine and Grasshoff (1975), Grasshoff (1988, 1992) and González (1993). In the Algarve coast, underwater identification of gorgonians is difficult because of ambiguities in the taxonomy of *Eunicella* and *Leptogorgia*, and therefore we used a set of criteria defined by Cúrdia et al. sub.b.

Multivariate methods were used to analyse the gorgonian communities at the studied areas. Non-metric multidimensional scaling was used to inbestigate differences in the distribution and abundance patterns of gorgonians across locations using the modified Gower dissimilarity index with transformed data ($\log_2 x + 1$). The modified Gower index (Anderson et al., 2006) is able to detect changes in composition but has the advantage of being directly interpretable as the average change in orders of magnitude (defined by the transformation). By using $\log_2$ transformation the modified Gower index is weighted towards a compositional change equal to a doubling in abundance (Anderson et al., 2006). Community composition differences between groups of samples were assessed using the non parametric multiple response permutation procedure (MRPP) (Zimmerman et al., 1985; Foster et al., 2009). Indicator species analysis (ISA) was performed to investigate the association of each gorgonian species to the studied areas, with the indicator species value (Dufrêne and Legendre, 1997) estimated using the index $\sqrt{IndVal^{g}_{ind}}$ (hereafter designated IndVal) proposed by De Cáceres et al. (2010). Differences in abundance between groups of samples were tested using the non parametric Wilcoxon rank-sum test. To quantify the ecological association of gorgonian species, three measures based on presence-absence data were used: Ochiai, Dice and Jaccard (Janson and Vegelius, 1981). The three measures range from 0 (when the two species being compared do not share any sample) to 1 (when the two species share all the samples). All statistical analyses were conducted using the open source software R version 12.1 (R Development Core Team, 2010).

2.2.4. Size-frequency distribution patterns

The size-frequency distribution patterns were analysed at the four sampling areas for *Eunicella gazella*, *Eunicella labiata*, *Leptogorgia lusitanica* and *Leptogorgia sarmentosa*. These species were selected because of their frequency of occurrence and abundance, as well as their relevance in differentiating gorgonian assemblages (see Results). For each species, all the colonies observed along linear transects were measured in order to prevent duplicates. The scuba diver dived close to the substratum in order not to miss the smallest colonies. The maximum height of each colony was measured to the nearest 0.5 cm and used as size parameter (Linares et al., 2008d).

The mean height of each species in each site both at shallow and deep sites was compared using the non-parametric Mann-Whitney U test. Size- frequency distribution of each gorgonian population was analysed using histograms and kernel density estimation (e.g. Everitt and Hothorn, 2006; Turley and Ford, 2011). The size-frequency distribution curve was analysed in terms of descriptive statistics using skewness and kurtosis (Linares et al., 2008d). Skewness (g1) is a measure of the symmetry of a distribution, being defined as the third moment of the distribution divided by its standard deviation (Legendre and Legendre, 1998). If skewness is significant, the distribution is asymmetric. Positive skewness corresponds to a frequency distribution with a longer "tail" to the right than to the left (prevalence of small size classes in the population), whereas a distribution with a longer "tail" to the left than to the right shows negative skewness (dominance of large size classes) (Legendre and Legendre, 1998). Kurtosis (g2) is a measure of the peakedness (or flatness) of a distribution near its central model, being defined as the fourth moment of the frequency distribution. A significant value of kurtosis indicates that the variable has longer tails than those for a normal distribution and therefore the prevalence of a particular size class in the population. Skewness and kurtosis coefficients are significant if g1 per SES (standard error of skewness) or g2 per SEK (standard error of kurtosis) is greater than 2 (Sokal and Rohlf, 1995). All statistical analyses were conducted using the open source software R version 12.1 (R Development Core Team, 2010).

2.3. Results

Gorgonians were very frequent in the study area being observed in more than 95 % of the transects sampled at each area. Eight gorgonian species were identified in the present study but *Paramuricea clavata*, *Eunicella singularis* and *Eunicella* sp. were rare and presented extremely low abundance (Table 2.3).

2.3.1. Gorgonian assemblages at the regional scale of the Algarve

Table 2.3.: Presence, frequency of occurrence (%) and density (colonies/5m^2) of the gorgonian taxa at the different locations. t - number of transects sampled; twg - transects with gorgonians; n - number of colonies; max. - maximum number of colonies in a single transect.

	All gorgonians			Species			Colonies		Density		
	t	twg	(%)		twg	(%)	n	(%)	Mean	SE	max.
Lagos shallow											
	72	69	(95.8)	*Eunicella gazella*	50	(69.4)	260	(24.1)	3.6	0.72	34
				Eunicella labiata	61	(84.7)	484	(44.9)	6.7	0.85	29
				Eunicella sp.	1	(1.4)	1	(0.1)	0.0	—	1
				Eunicella verrucosa	48	(66.7)	181	(16.8)	2.5	0.59	19
				Leptogorgia lusitanica	16	(22.2)	26	(2.4)	0.4	0.23	4
				Leptogorgia sarmentosa	35	(48.6)	125	(11.6)	1.7	0.57	15
Lagos deep											
	30	29	(96.7)	*Eunicella gazella*	23	(76.7)	153	(14.4)	5.1	1.78	38
				Eunicella labiata	29	(96.7)	327	(30.7)	10.9	2.43	55
				Eunicella verrucosa	26	(86.7)	264	(24.8)	8.8	2.19	39
				Leptogorgia lusitanica	9	(30.0)	30	(2.8)	1.0	0.60	6
				Leptogorgia sarmentosa	24	(80.0)	291	(27.3)	9.7	2.18	42
Pedra da Greta											
	20	20	(100.0)	*Eunicella gazella*	19	(95.0)	265	(45.5)	13.2	2.37	48
				Eunicella labiata	18	(90.0)	63	(10.8)	3.1	0.51	8
				Eunicella singularis	1	(5.0)	1	(0.2)	0.0	—	1
				Eunicella verrucosa	15	(75.0)	62	(10.6)	3.1	0.77	11
				Leptogorgia lusitanica	20	(100.0)	181	(31.0)	9.1	1.90	41
				Leptogorgia sarmentosa	4	(20.0)	11	(1.9)	0.6	0.31	5
Pedra do Barril											
	12	12	(100.0)	*Eunicella gazella*	12	(100.0)	377	(50.4)	31.4	3.68	53
				Eunicella labiata	12	(100.0)	219	(29.3)	18.2	1.78	30
				Eunicella verrucosa	3	(25.0)	3	(0.4)	0.2	0.00	1
				Leptogorgia lusitanica	12	(100.0)	120	(16.0)	10.0	2.58	27
				Leptogorgia sarmentosa	10	(83.3)	24	(3.2)	2.0	0.54	6
				Paramuricea clavata	3	(25.0)	5	(0.7)	0.4	0.67	3

Gorgonian assemblages were mainly composed of: three *Eunicella* species, *Eunicella labiata*, *Eunicella gazella* and *Eunicella verrucosa*; and two *Leptogorgia* species, *Leptogorgia lusitanica* and *Leptogorgia sarmentosa*. The density of gorgonians was extremely variable but the above mentioned species commonly presented dense aggregations of conspecifics. Besides, these species were highly associated in the study area as they were commonly observed at the same transects Figure 2.2. Within each assemblage, the dominant species presented high similarity between themselves, whereas the less abundant and frequent species presented lower values. This pattern was particularly evident in Lagos Bay at both depths, where *Leptogorgia lusitanica* presented low abundance (2.4 % and 2.8 % of the total, for shallow and deep sites, respectively) and was less frequent (present in 22 % and 30 % of the sampled transects, respectively). The same pattern was found for *Leptogorgia sarmentosa* in Pedra da Greta and for *Eunicella verrucosa* in

Pedra do Barril.

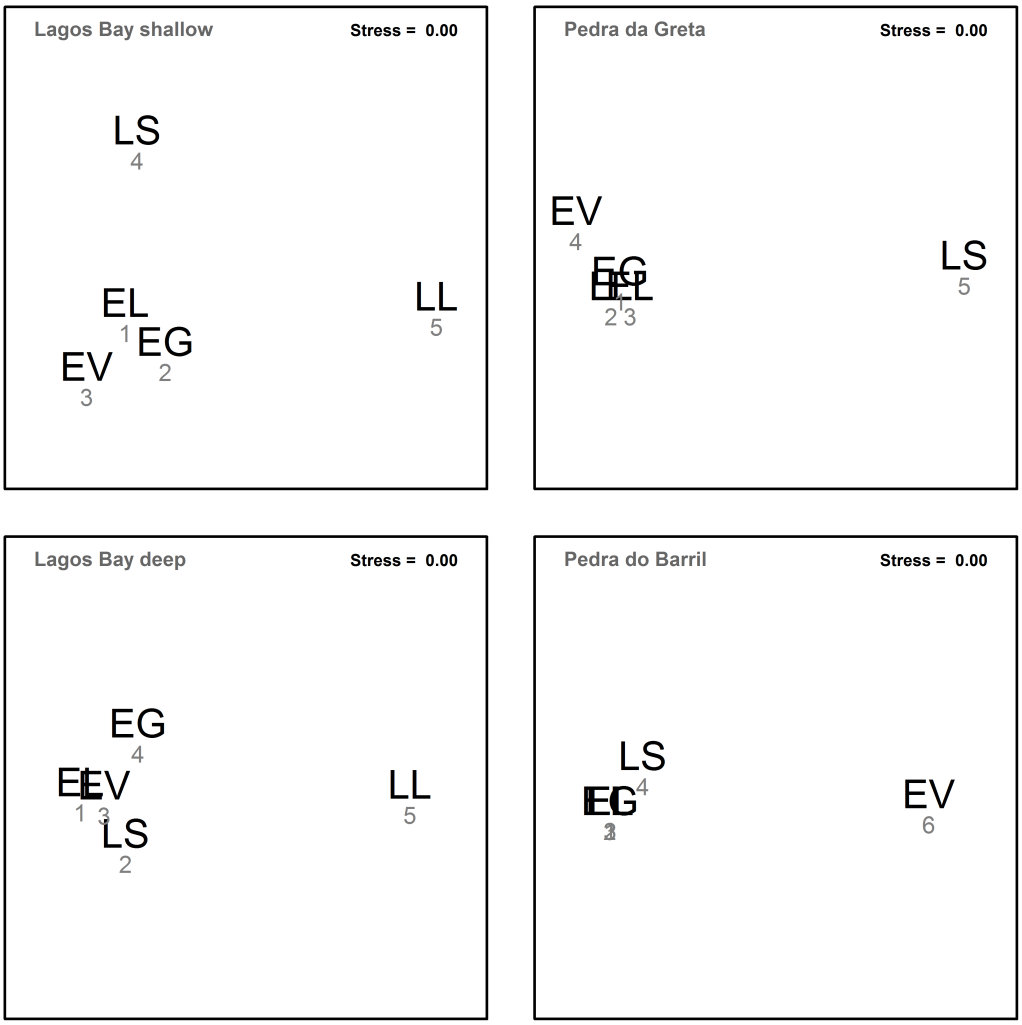

Figure 2.2.: Non-metric multidimensional scaling plot of the association of gorgonian species at each assemblage. Ochiai similarity on presence/absence data. Grey numbers below species label indicates the abundance rank of the species in the assemblage. EG – *Eunicella gazella*, EL – *Eunicella labiata*, EV – *Eunicella verrucosa*, LL – *Leptogorgia lusitanica* and LS – *Leptogorgia sarmentosa*.

The non metric multidimensional scaling (nMDS) ordination plot showed three main clusters: one large cluster aggregating the samples from Lagos Bay and two smaller clusters comprising the samples of Pedra da Greta and Pedra do Barril (Figure 2.3). The superimposition of total abundance and number of species data evidenced a gradient from the lower left corner to the upper right corner of the plot (Figure 2.3, Abundance and Number of Species). The indicator species analysis (ISA) indicated that *Eunicella labiata* was common and abundant at all sampled areas (IndVal=0.959) but that *Paramuricea clavata* was exclusive of Pedra do Barril (IndVal=0.500, $p = 0.003$). *Leptogorgia sarmentosa* was mainly associated with deeper sites (Lagos deep and Pedra

do Barril, IndVal=0.816, $p = 0.001$), whereas two species were more characteristic of the Sotavento (Pedra da Greta and Pedra do Barril), namely *Leptogorgia lusitanica* (IndVal=0.963, $p = 0.001$) and *Eunicella gazella* (IndVal=0.907, $p = 0.001$). *Eunicella verrucosa* was common at Lagos shallow, Lagos deep and Pedra da Greta (IndVal=0.853, $p = 0.001$). The ISA results were also reinforced by the patterns evidenced when the abundance data of each gorgonian species was superimposed to the nMDS ordination plot (Figure 2.3).

The multiple response permutation procedures (MRPP) detected differences in the structure of the assemblages for several sources of variation (Table 2.4). It is noteworthy that multivariate dispersion was different between the samples of the Barlavento and the samples of Sotavento (Table 2.4), thus the differences observed with MRPP may be due to differences in dispersion and not to differences in the structure of the community. The assemblage structure was different between Barlavento and Sotavento, namely because of the significantly higher density of *Eunicella gazella* and *Leptogorgia lusitanica* in Sotavento (Tables 2.3 and 2.4 and Figure 2.3). Depth also influenced the structure of gorgonian assemblages, as *Eunicella labiata* and *Leptogorgia sarmentosa* were more frequent and presented higher density at deeper sites. In Barlavento, the occurrence and density of *Eunicella verrucosa* was also higher at deeper sites (Tables 2.3 and 2.4). On the other hand, in Sotavento the latter species presented lower density at deeper sites and was observed only in 25 % of the transects. What is more, *Eunicella gazella* also presented higher density at deeper sites in Sotavento. Comparing the samples at similar depth ranges at lower depth, *Eunicella labiata* and *Leptogorgia sarmentosa* presented lower density in the Sotavento (Pedra da Greta), with the latter species also showing lower occurrence rates (Table 2.3). In addition to the previously mentioned general pattern between Barlavento and Sotavento, the differences in gorgonian assemblages between Lagos deep and Pedra do Barril were due to *Eunicella labiata*, which was more abundant in Pedra do Barril, and *Eunicella verrucosa*, which was rare in this area.

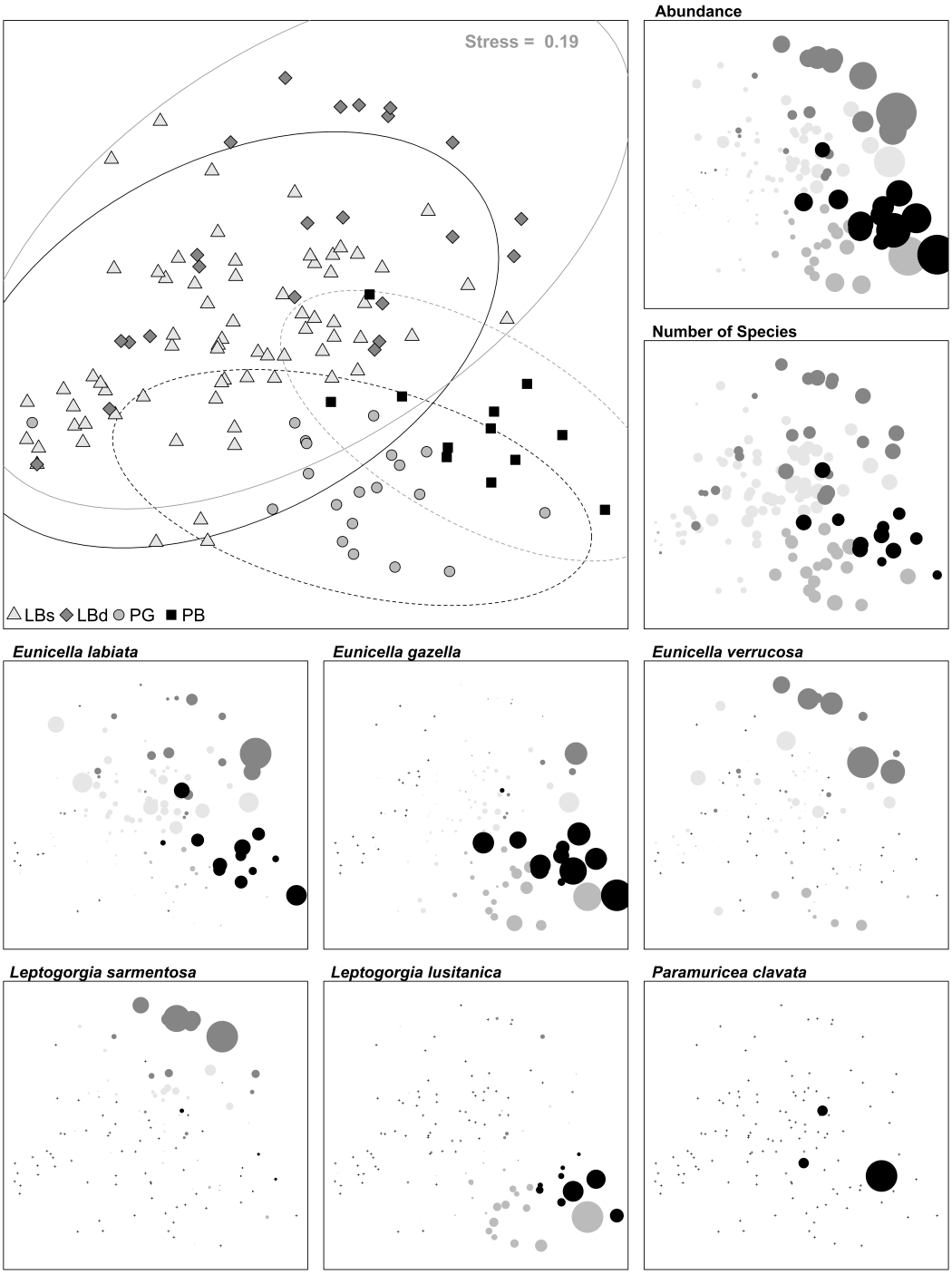

Figure 2.3.: Non-metric multidimensional scaling plot of the gorgonian community data (Lagos shallow - LB_S; Lagos deep - LB_D; Pedra da Greta - PG; Pedra do Barril - PB), using modified Gower index of dissimilarity on $\log_2(x+1)$ transformed data. Abundance data was superimposed to the ordination for each gorgonian species (for clarification purposes, the maximum size of the bubbles varies across plots). + – sample without colonies.

Table 2.4.: Multi response permutation procedures (MRPP) used to compare groups of samples. Permutation dispersion (z) for each set of samples. Median and mean values and Wilcoxon rank sum tests (W) for the most abundant gorgonian species. LB_S - Lagos shallow; LB_D - Lagos deep; PG - Pedra da Greta; PB - Pedra do Barril.

Source of variability	**Species**	**Median**		W	p	**Mean**		
Barlavento vs. Sotavento		$LB_S + LB_D$	$PG + PB$			$LB_S + LB_D$	$PG + PB$	
$A = 0.109$ $p = 0.001^{***}$	*E. gazella*	2	16	343.5	0.000	4.0	20.1	↗
$z = 4.82$ $p = 0.028^{*}$	*E. labiata*	5	5	1541.0	0.634	8.0	8.8	
	E. verrucosa	2	1	1981.0	0.063	4.4	2.0	
	L. lusitanica	0	8	122.0	0.000	0.6	9.4	↗
	L. sarmentosa	1	0	2001.0	0.042	4.1	1.1	↘
Shallow vs. Deep		Shallow	Deep			Shallow	Deep	
$A = 0.032$ $p = 0.001^{***}$	*E. gazella*	4	5.5	2289.5	0.084	5.7	12.6	
$z = 5.86$ $p = 0.022^{*}$	*E. labiata*	4	10	2743.5	0.000	5.9	13.0	↗
	E. verrucosa	1	2	2199.0	0.191	2.6	6.4	
	L. lusitanica	0	0.5	2193.0	0.164	2.2	3.6	
	L. sarmentosa	0	4	2955.0	0.000	1.5	7.5	↗
within Barlavento								
LB_S vs. LB_D		LB_S	LB_D			LB_S	LB_D	
$A = 0.036$ $p = 0.001^{***}$	*E. gazella*	3	2	1115.0	0.794	3.6	5.1	
$z = 2.40$ $p = 0.129$	*E. labiata*	5	5.5	1277.5	0.146	6.7	10.9	
	E. verrucosa	1	3.5	1558.5	0.000	2.5	8.8	↗
	L. lusitanica	0	0	1207.5	0.214	0.4	1.0	
	L. sarmentosa	0	6.5	1683.5	0.000	1.7	9.7	↗
within Sotavento								
PG vs. PB		PG	PB			PG	PB	
$A = 0.183$ $p = 0.001^{***}$	*E. gazella*	11	33	208.5	0.000	13.3	31.4	↗
$z = 2.07$ $p = 0.188$	*E. labiata*	3	19	239.0	0.000	3.1	18.3	↗
	E. verrucosa	2	0	42.0	0.001	3.1	0.3	↘
	L. lusitanica	8.5	7.5	118.5	0.962	9.1	10.0	
	L. sarmentosa	0	1.5	195.0	0.001	0.6	2.0	↗
within Shallow								
LB_S vs. PG		LB_S	PG			LB_S	PG	
$A = 0.108$ $p = 0.001^{***}$	*E. gazella*	3	11	199.0	0.000	3.6	13.3	↗
$z = 4.63$ $p = 0.041^{*}$	*E. labiata*	5	3	929.5	0.046	6.7	3.1	↘
	E. verrucosa	1	2	601.0	0.249	2.5	3.1	
	L. lusitanica	0	8.5	24.0	0.000	0.4	9.1	↗
	L. sarmentosa	0	0	923.0	0.031	1.7	0.6	↘
within Deep								
LB_D vs. PB		LB_D	PB			LB_D	PB	
$A = 0.223$ $p = 0.001^{***}$	*E. gazella*	2	33	16.5	0.000	5.1	31.4	↗
$z = 19.25$ $p = 0.001^{***}$	*E. labiata*	5.5	19	67.5	0.001	10.9	18.3	↗
	E. verrucosa	3.5	0	325.5	0.000	8.8	0.3	↘
	L. lusitanica	0	7.5	26.0	0.000	1.0	10.0	↗
	L. sarmentosa	6.5	1.5	262.5	0.020	9.7	2.0	↘

2.3.2. Size-frequency distributions

The sample size varied between sites depending greatly on the density of each species at each site. The height of *Eunicella gazella*, *Leptogorgia lusitanica* and *Leptogorgia sarmentosa* at 15–20 m (shallow sites) was significantly lower in Pedra da Greta, where fishing is more intensive (Table 2.5) but the opposite trend was observed concerning *Eunicella labiata* presenting taller colonies in this location. Concerning the deeper populations, the pattern was different: *Eunicella labiata* did not present significant differences between populations, whereas the populations of the remaining species from the less fished area (Lagos deep) presented a significantly lower height than in Pedra do Barril.

The distributions of *Eunicella gazella* sizes were positively skewed with the exception of Lagos shallow which is symmetric. However, only the population of Pedra do Barril presented a distribution that is more peaked than a normal distribution (see Figure 2.4 and Table 2.5). The other *Eunicella* species presented symmetric distributions at all sampled sites but the distributions in the populations of the less fished areas (Lagos Bay) were less peaked than a normal distribution, as they showed significant negative kurtosis. Similarly to *Eunicella gazella*, the distribution of sizes of *Leptogorgia lusitanica*, except for the population of Lagos shallow, were asymmetric, presenting significant positive skewness values (deviated towards small sizes). This species presented negative kurtosis for the population of Lagos shallow, and positive kurtosis for the remaining populations; yet only the population from Pedra da Greta presented significant kurtosis (more peaked than a normal distribution; Figure 2.4 and Table 2.5). The populations of *Leptogorgia sarmentosa* were symmetric in the less fished areas and asymmetric in the fished areas, where positively skewed distributions were oberved (towards small sizes). However, only the population from Pedra da Greta presented a significant kurtosis, showing a more peaked distribution (due to the high number of small sized colonies <10 cm).

Size-frequency distributions for *Leptogorgia lusitanica*, *Leptogorgia sarmentosa*, *Eunicella gazella* and *Eunicella labiata* populations at Lagos shallow, Pedra da Greta and Pedra do Barril were generally unimodal, and more or less bell-shaped (Figure 2.4). However, the four gorgonian species seem to present a bimodal distribution at Lagos deep with a large contribution of small sizes for all species (<5 cm for *Eunicella gazella*; <10 cm for *Eunicella labiata*, *Leptogorgia lusitanica* and *Leptogorgia sarmentosa*). At this site, *Eunicella labiata* is the only species whose population is not clearly dominated by small sizes, presenting a peak at ≈40 cm (the major peak of the distribution).

Table 2.5.: Statistics of the sampled populations (mean, median, sample size (n), Mann-Whitney U test (*U* and p-value), minimum (Min), maximum (Max), skewness (g1, with SE and significance) and kurtosis (g2, with SE and significance) for *Eunicella gazella*, *Eunicella labiata*, *Leptogorgia lusitanica* and *Leptogorgia sarmentosa*. Values presented in bold represent significant skewness and kurtosis.

Species	Site	Mean	Median	n	*U*	p-value	Min	Max	g1	SE g1	Sig. g1	g2	SE g2	Sig. g2
Lagos shallow *vs.* Pedra da Greta														
E. gazella	LB_S	13.2	13	78	8676	**<0.001**	5	21	0.139	0.2722	0.5110	-0.832	0.5382	-1.5454
	PG	9.1	9	149			1	22	0.500	0.1987	**2.5168**	-0.513	0.3949	-1.2995
E. labiata	LB_S	23.9	23	119	5551	**<0.001**	5	47	0.239	0.2218	1.0780	-1.052	0.4401	**-2.3894**
	PG	36.1	36.5	202			1	66	-0.208	0.1711	-1.2150	0.182	0.3405	0.5331
L. lusitanica	LB_S	29.1	28.5	30	3600	**<0.001**	15	48	0.437	0.4269	1.0248	-0.701	0.8327	-0.8420
	PG	7.9	4	128			2	40	2.050	0.2140	**9.5779**	**3.136**	0.4249	**7.3803**
L. sarmentosa	LB_S	33.1	31	34	1710.5	**<0.001**	12	62	0.567	0.4031	1.4059	0.035	0.7879	0.0450
	PG	16.7	13	58			3	63	1.472	0.3137	**4.6915**	2.798	0.6181	**4.5258**
Lagos deep *vs.* Pedra do Barril														
E. gazella	LB_D	5.8	3	60	900	**<0.001**	0.5	20	1.019	0.3087	**3.3009**	-0.363	0.6085	-0.5958
	PB	9.9	9	60			4	25	0.946	0.3087	**3.0658**	1.409	0.6085	**2.3164**
E. labiata	LB_D	26.8	27	119	15990	0.4013	1.5	64	0.174	0.2218	0.7844	-1.069	0.4401	**-2.4300**
	PB	25.1	25	255			3	52	0.132	0.1525	0.8656	0.203	0.3038	0.6669
L. lusitanica	LB_D	17.8	11.5	37	822	**0.0143**	4	66	1.132	0.3876	**2.9214**	0.700	0.7587	0.9229
	PB	22.0	20	63			5	51	0.882	0.3016	**2.9242**	0.436	0.5948	0.7332
L. sarmentosa	LB_D	18.2	13.8	19	215.5	**0.0077**	4	42	0.460	0.5238	0.8776	-1.364	1.0143	-1.3453
	PB	29.2	26.5	40			7	67	0.847	0.3738	**2.2661**	0.052	0.7326	0.0707

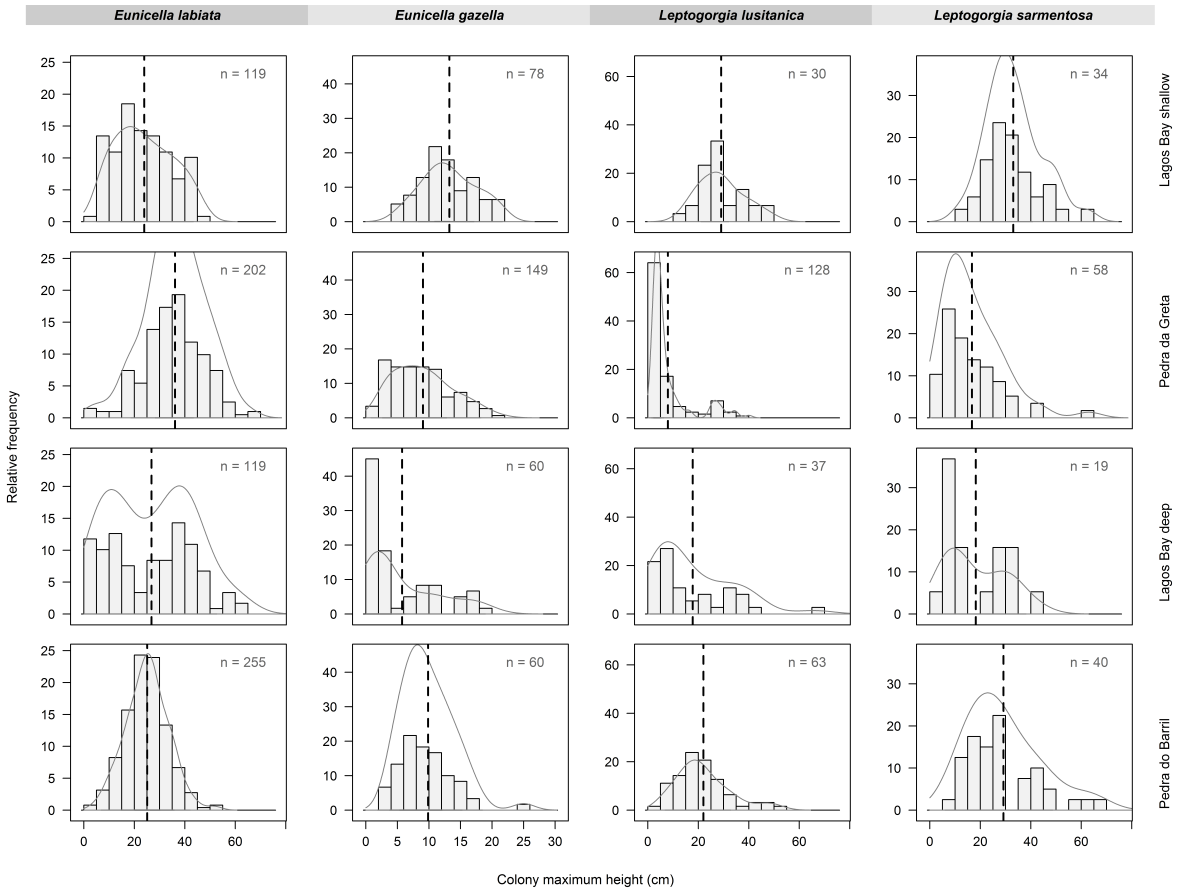

Figure 2.4.: Relative frequency of maximum colony height of *Eunicella gazella, Eunicella labiata, Leptogorgia lusitanica, Leptogorgia sarmentosa* populations from shallow (Lagos shallow and Pedra da Greta) and deep sites (Lagos deep and Pedra do Barril). Kernel density estimation curves are also presented (area below the curve integrates to unity). Dashed vertical lines represent each population's mean height.

2.4. Discussion

The gorgonian fauna of the southern Portuguese coast is composed by species of different origins, namely from the Atlantic (*Eunicella verrucosa*), Mediterranean (*Leptogorgia sarmentosa, Eunicella singularis, Paramuricea clavata*) and North Africa (*Eunicella labiata, Eunicella gazella*), highlighting the importance of this geographical area for the fluxes of biological diversity, namely those of long lived animals with a relevant role in the benthic ecosystem functioning. The inexistence of previous quantitative studies in the study area hampers comparisons and consequently the assessment of potential changes in abundance and structure of gorgonian fauna. Some remarkable differences, however, emerged from the comparison with the Mediterranean area. While the western Mediterranean assemblages are mainly monospecific (Bianchi, 2007; Gori et al., 2011a), in the Algarve, diversity is higher, similarly to the observed in tropical areas (Lasker and

Coffroth, 1983; Yoshioka and Yoshioka, 1989; Chiappone et al., 2003). Besides, in the Mediterranean area, species rarely coexist (Gori et al., 2011a), whereas in the south coast of Portugal, there is a high association of several gorgonian species that co-dominate the assemblages. The five dominant species, *Eunicella gazella*, *Eunicella labiata*, *Eunicella verrucosa*, *Leptogorgia lusitanica* and *Leptogorgia sarmentosa* were also found to be abundant and to co-occur in several locations in the Alborán Sea, near the entrance of the Mediterranean (Ocaña et al., 2000). Contrastingly, in the neighbouring western Mediterranean waters, gorgonian assemblages are generally dominated by *Paramuricea clavata* or *Eunicella singularis* with *Eunicella cavolinii* and *Leptogorgia sarmentosa* also being common and abundant (e.g. Coma et al., 2004, 2006; Linares et al., 2008a; Garrabou et al., 2009; Gori et al., 2011a). Except for *Leptogorgia sarmentosa*, the remaining species are entirely absent or rare and presenting low abundance in the Algarve, showing once more a remarkable resemblance to the patterns observed near Gibraltar and the Alborán Sea (González, 1993; Ocaña et al., 2000). The present results reinforce the importance of areas under the influence of different water masses and oceanographic curents for marine biodiversity and conservation (Bianchi, 2007; Carvalho et al., in press).

2.4.1. Observed distribution and ecology of gorgonians

Despite the co-existence of the main species, some spatial differences in the abundance patterns were observed along the southern coast of Portugal that may be related to different environmental requirements of the species but also to a higher fishing pressure in the Sotavento. For example, *Eunicella gazella* and *Leptogorgia lusitanica* were more abundant in fished areas, while the abundance of *Eunicella labiata* and *Leptogorgia sarmentosa* was greater in less fished areas. The abundance of gorgonians increased with depth, in line with reports of other geographical areas (e.g. Stone, 2006; Linares et al., 2008a; Gori et al., 2011a), but also for the south of Portugal (Cúrdia et al., sub.b). Physical complexity of the substrate is very different at the sampled areas, increasing from Lagos Bay to Pedra da Greta. At Pedra do Barril, intermediate complexity levels were observed, as canyons cutting the rocky formations were less common and less heterogeneous than in Pedra da Greta, but rocky formations generally presented higher elevation from the seabed (3–5 m). Contrastingly, turbidity showed the opposite trend being higher at Lagos Bay, probably because of the proximity of the mouth of the Arade and Bensafrim estuaries and the Ria de Alvor coastal lagoon. These observations support the distribution pattern of *Leptogorgia sarmentosa*, which abundance was significantly higher in Lagos Bay than in the other studied areas. This species has been pointed out as indicator of silt (Weinberg, 1978) and characteristic of horizontal or sloped surfaces where sediment tend to accumulate or even of soft-bottoms (González, 1993; Gori et al., 2011a); it is also typical of areas of moderate disturbance where sediment re-suspension is high (Ribes et al., 2003; Rossi et al., 2004; Gori et al., 2011a). The habitat conditions in Lagos Bay clearly favour this species as the area is characterized by low relief rocky plateaus with a thick

layer of fine sediment particles that are easily re-suspended (submerged rock bottoms). On the other hand, the few *Leptogorgia sarmentosa* observed in Pedra da Greta were found in horizontal surfaces of rock with low relief and close to sandy areas (in the reef margins and in sand pockets) or in isolated rocks between large blocks. The intermediate abundance values found at Pedra do Barril together with the intermediate values of sediment bed load reinforce the influence of this environmental parameter as a driving force in structuring *Leptogorgia sarmentosa* assemblages, which is supported by the importance of re-suspended particles in the diet of this species (Ribes et al., 2003; Rossi et al., 2004). Even though the environmental conditions at Lagos Bay seemed to be highly favourable for *Leptogorgia sarmentosa* assemblages, its mean abundance at 20–25 m depth (1.94 colonies m^{-2}) was similar to the maximum density values reported by Gori et al. (2011a, 1.5 colonies m^{-2}), but much lower than the 17 colonies m^{-2} found by Weinberg (1978) and Mistri (1995) in other western Mediterranean areas. However, the maintenance of population at intermediate abundance levels may be a strategy of the species to overcome potential abrasion effects caused by water movement, as *Leptogorgia sarmentosa* is characterised by thin and flexible branches, and therefore, dense populations are more likely affected by abrasion (Tsounis et al., 2006).

Ecological requirement of the remaining species are still poorly acknowledged. However, it is known that, for example, *Leptogorgia lusitanica* prefers habitats with some hydrodynamics but clear waters (González, 1993), which is consistent to the present dataset. In opposition to the observed for *Leptogorgia sarmentosa*, higher densities of *Leptogorgia lusitanica* were observed in Pedra da Greta and Pedra do Barril when compared to Lagos Bay, where turbidity was higher. On the other hand, sedimentation and turbidity do not seem to affect the establishment and succession of *Eunicella* species, particularly *Eunicella labiata*, which seems to have the ability to tolerate different levels of sedimentation, generally presenting high abundance and/or being a top ranked species in areas subjected to different levels of sedimentation. *Eunicella verrucosa*, although distributed along the southern Portuguese coast, was more common and abundant in Lagos Bay and Pedra da Greta than in Pedra do Barril. This distribution pattern may reflect its habitat requisites, as this species has been described as relatively sciaphilic, living in hard bottom habitats (Carpine and Grasshoff, 1975), sloped rocky blocks and on small rocks and shells in detritic bottoms (González, 1993), which were rare in the sites sampled in Pedra do Barril. What is more, this species and *Leptogorgia sarmentosa* have been commonly found in shallow waters in western Mediterranean in areas with increased turbidity (Sartoretto and Francour, 2012).

The low abundance and frequency of occurrence of *Eunicella singularis* and *Paramuricea clavata* was expected as these are typical Mediterranean species. *Paramuricea clavata* was only accounted in Pedra do Barril, especially in vertical walls, but with low abundance (although not observed in this study, this species has been also occasionally observed in Pedra da Greta and in Lagos Bay). These observations are consistent with reports from the Mediterranean,

where *Paramuricea clavata* is extremely abundant in vertical walls at similar depths (Linares et al., 2008a; Gori et al., 2011a), reaching densities of 52.5 colonies m^2 (Linares et al., 2008d). *Paramuricea clavata* presents a narrow range of environmental requirements, such as irradiance and sedimentation (Linares et al., 2008a). The latter factor has been suggested as determinant for the variation of its upper limit depth along the Mediterranean Spanish coast, being reported from southern sites at similar depth to Pedra do Barril, around 25–30 m depth (Linares et al., 2008a). In Portuguese waters, this species has been observed outside the study area, in Professor Luiz Saldanha Marine Park (Arrábida, Center of the western Portuguese coast) (Rodrigues, 2008), Ilha das Berlengas (Center/North of the western Portuguese coast) (Rodrigues et al., 2008) where it is found in large densities in vertical walls (J G, personal observation) and in the submarine mountains of the Gorringe Bank (Anonymous, 2006b). Recently, it has been reported that in southern Portugal, *Paramuricea clavata* dominates the gorgonian assemblage at 59–120 m depth (Anonymous, 2011). Taking into consideration that the present study accounted for shallow waters only, the distribution of *Paramuricea clavata* in the Algarve may be underestimated, highlighting the need for further studies at deeper depths. In the case of *Eunicella singularis*, which is very abundant in the Mediterranean (Ballesteros, 2006; Gori et al., 2011a), displaying great plasticity and amplitude in its environmental preferences (Gori et al., 2011a), its low occurrence and abundance may be related to the generally lower light intensity of the Algarve mesotrophic waters when compared to the oligotrophic Mediterranean waters. Shallow colonies of *Eunicella singularis* host zooxanthelae and consequently have a marked dependence on light (Previati et al., 2010; Gori et al., 2011b).

2.4.2. Impacts on shallow water gorgonians: anthropogenic versus natural disturbance

In the study area, fishing and anchoring seem to be the most potentially injurious anthropogenic disturbance events affecting gorgonian assemblages. Besides, based on several statistics, fishing pressure is higher in the Sotavento than in Barlavento. In situ observations during surveys support this idea, as in areas under higher fishing pressure, gorgonian colonies detached from the bottom and covered with sediment were frequently observed. Contrary to some gorgonians that reattach and recover after disturbance events, the recovery of detached gorgonians in the Algarve seems to be low, similarly to what has been reported from the Mediterranean (Linares et al., 2008d).

Differences in gorgonian density over the studied areas may be a consequence of the interaction of both natural and anthropogenic pressures, which is supported by the size-frequency distribution of the main gorgonian species. Gorgonian populations sampled in more intensively fished areas generally presented skewed distributions towards small sizes, and more peaked than normal distributions suggesting that these populations are affected by disturbance events. However,

in the studied populations, gorgonians of higher sizes were not restricted to the sites under lower pressure, as observed for other soft corals where larger sizes are found in more pristine sites (Linares et al., 2008a, and references therein). The survival of large-sized colonies play an important role in the persistence of gorgonian populations, compensating for poor reproductive success (Yoshioka, 1998) and, therefore, this item should always integrate management plans.

On the other hand, the present data showed that all gorgonian populations in Lagos deep presented bimodal distributions, suggesting a disturbance event that eradicated part of the populations and/or severely affected recruitment over time. This site was characterized by a thick layer (1–3 cm) of fluidised sediment, which totally covered many small sized gorgonian colonies that presented retracted polyps. Considering the location and the environmental characteristics of the site, the most probable disturbance was high loads of sediments distributed over the seabed, most coming from the Arade river, that are easily re-suspended (see Airoldi, 2003, for a review). Data on recruitment, natural mortality and growth rates for the Algarve are completely unavailable, therefore it is impossible to ascertain if the disturbance was punctual or repeated in time. These observations lead us to hypothesize that disturbance event(s) resulting in a large accumulation of sediments in shallow rocky bottoms may affect gorgonian populations, namely by affecting small sized specimens and preventing recruitment or at least imposing high mortality of recruits, producing gaps in size-frequency distributions. The current results also suggest that spatially close areas under similar anthropogenic pressure may present different demographic patterns if subjected to different environmental conditions. Indeed, no significant skewness or kurtosis for the four studied populations were detected in Lagos shallow, suggesting lower natural disturbance than in Lagos deep. This pattern is similar to those of population of *Eunicella singularis* and *Paramuricea clavata* from the Mediterranean (Linares et al., 2008a). What is more, at this site the height of gorgonians was significantly higher than all (*Eunicella gazella* and *Leptogorgia lusitanica*) or part (*Leptogorgia sarmentosa*) of the remaining populations. On the other hand, the positive skewness values found in Pedra da Greta, Pedra do Barril and Lagos deep point towards some disturbance, either anthropogenic (fishing/anchoring) or natural (sediment run-off), which is in line with the observed in the Mediterranean (Linares et al., 2008a) but not with other studies that suggest negative skewness values in disturbed areas (Bak and Meesters, 1998; Meesters et al., 2001).

The present data suggest that different species respond differently to disturbance: *Eunicella labiata* sizes do not seem to be affected; *Eunicella gazella* and *Leptogorgia lusitanica* seem to be affected by both kinds of stress; and *Leptogorgia sarmentosa* seems to be affected mainly by anthropogenic activities. Direct mortality rates caused by disturbance may often be low and not clearly depicted by size-frequency distributions. However, disturbance may significantly impact marine species by reducing the fitness and alter energy investment of marine animals, being an important issue in fisheries (Gaspar and Chícharo, 2007; Shester and Micheli, 2011). In fact, concerning gorgonians, mortality can be increased due to vulnerability to diseases and fouling

and regeneration consumes energy that cannot be directed to reproduction and growth, resulting in reduced reproductive output, low dispersion and low growth rates (Linares et al., 2008c). Even though size-frequency distribution data of *Eunicella labiata* did not show significant skewness and kurtosis, it was observed that partial mortality in *Eunicella gazella* and *Eunicella labiata* was higher in more intensively fished areas than in areas under lower fishing pressure (unpublished data). Specifically concerning *Eunicella labiata*, the most frequent damage involved the complete breaking of one of the two main branches of the colony, not severely affecting the size parameter that was measured (height), but certainly affecting the biological and ecological aspects of the species. As suggested by Linares et al. (2008a) and the present data, it is important that size-frequency distribution data is complemented by damage quantification data in order to properly assess disturbance effects in gorgonian corals.

2.4.3. Final remarks

The gorgonian assemblages in shallow rocky areas of the Algarve were found to be more diverse than those of the Mediterranean area, with several dominant species coexisting. The intricate differences in ecological requirements and resilience to disturbance of gorgonian species shape their populations with important effects in the dynamics and biodiversity of shallow rocky communities. Some studies suggest that communities with more species of ecosystem or habitat engineers present higher biodiversity and are more resilient (Coleman and Williams, 2002), which reinforces the relevance of the present study area in the context of NE Atlantic biodiversity.

The key role of gorgonians for the community of the infra- and circalittoral rock poses another challenge, the capacity of these animals to cope with both thermal stress but also pathogens under climate change, an important issue in the future management of coastal marine ecosystems. The high abundance of two *Eunicella* species (*Eunicella labiata* and *Eunicella gazella*) characteristic of the African coast, but that are also present in the Mediterranean (González, 1993; Ocaña et al., 2000), or in the case of *Eunicella gazella* also in the Northern coast of Spain (Grasshoff, 1992), may indicate that these species, original from lower latitudes, are extending their distribution northwards. In Europe, the increasing sea water temperature as a result of climate change is inducing the spread of numerous tropical marine species (see references in Bianchi, 2007; Philippart et al., 2011) presenting new scientific and coastal management challenges (Anna, 2007). Data on genetic diversity on these gorgonian species could prove if these species are recent colonizers or if they have established long time ago and have been overlooked due to erroneous identifications. Furthermore, climate change has been pointed out as the primary responsible for: i) benthic fauna mass mortality events in the Mediterranean (Coma et al., 2009; Lejeusne et al., 2010, and references therein); ii) changes on the reproduction of coastal invertebrates (Lawrence and Soame, 2004), namely octocorals (Linares et al., 2008c); iii) the increase of pathogenic diseases

in gorgonians (Martin et al., 2002; Bally and Garrabou, 2007); iv) changes on growth rates and population structure of corals (Goffredo et al., 2008); and v) changes in calcification rates of gorgonians (Ferrier-Pagès et al., 2009). Thermotolerance of gorgonians has been observed to be depth dependent (Teixidó et al., 2011) emphasizing the importance of spatial distribution data in areas affected by multiple pressures.

In order to fully understand the factors that might be affecting the distribution of gorgonians in the Algarve, more studies shall be undertaken, with broader scales and complemented by environmental data and quantitative video-surveys (e.g. on underwater lost fishing gears). As an example, the use of modern technology such as ROVs has been used to provide solid data concerning corals distribution at mid and deeper waters impossible to sample by scuba diving (e.g. Mortensen and Buhl-Mortensen, 2004; Gori et al., 2011a). Quantitative data on fishing effort per area, and number of lost fishing gears is also important for a more robust interpretation of the direct and indirect effects of fishing in gorgonian populations. As evidenced by this study, gorgonian size-frequency distributions can be used as proxy for disturbance effects as these slow growing long-lived animals can be used as natural data loggers, registering disturbances along time. However, in order to discriminate between natural and anthropogenic disturbances, size-frequency data should be complemented by information on secondary colonization and partial mortality. In this context, the present study provides valuable baseline information that may be used in future monitoring programs.

Acknowledgements

J.C. (SFRH/BD/29491/2006) benefits from a PhD grant from the “Fundação para a Ciência e a Tecnologia” (FCT)’. Project Rensub (http://www.rensub.com) supported part of this study and was funded by ARH Algarve and POVT.

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Part II.

Gorgonians and their associated epibenthic fauna

CHAPTER 3

Diving into shallow-temperate gorgonian gardens: biodiversity patterns of attendant epifaunal assemblages across multiple scales of variability

Submitted to: *Marine Ecology Progress Series*

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Abstract

To date, few studies have examined the relationship between gorgonians and associated non-colonial epifaunal assemblages, especially in temperate Atlantic waters. Two species belonging to two widespread octocoral genera (*Leptogorgia* and *Eunicella*) were selected aiming to assess the variation in composition and structure of their associated epifaunal assemblages with colony size and host species, as well as to analyse the consistency in space and time of these putative patterns. One hundred and eighty-one species from 11 different phyla (totalling 7284 individuals) were identified in 72 replicate colonies. A single colony of *Leptogorgia lusitanica*, approximately 23 cm width, harboured more than 730 individuals from 63 species. The maximum abundance in *Eunicella gazella* (358 individuals) was recorded in a colony of approximately 11 cm width, while the peak of diversity (55 species) was registered in a larger colony of 23.6 cm width. The epifaunal assemblages of both gorgonian species were numerically dominated by amphipods, whereas in terms of diversity, annelids (especially polychaetes) were the richest group in *Eunicella gazella* colonies. The RDA analysis indicated a strong relationship of all the size-related attributes (area, maximum width and height) and *Leptogorgia lusitanica* epifaunal assemblages, but the "colonial" epibiont cover (e.g. macroscopic algae, bryozoans, sponges) was also observed to be determinant in structuring the attendant epifaunal assemblages of both gorgonian species. Epifaunal assemblage structure differed between gorgonian species with a single taxon (Turbellaria) significantly associated with *Eunicella gazella* colonies and taxa indicated as significantly associated with *Leptogorgia lusitanica* colonies. Although both gorgonians shared most of the species collected, 11 and 18 taxa were exclusively associated with *Eunicella gazella* and *Leptogorgia lusitanica*, respectively (without considering singletons). Nevertheless, most of these exclusive taxa were either rare or uncommon. The exception was the presence of white flatworms Turbellaria in *Eunicella gazella* colonies probably taking advantage of crypsis with the white *Eunicella gazella* branches. The present study supports the general paradigm that corals (generally for scleractinian corals) are habitats of enhanced abundance and biodiversity. Gorgonian epifaunal assemblages not only showed high values of α-diversity but intricate patterns of variability in their composition and structure leading to high β-diversity. Higher β-diversity values were consistently detected for raw than for presence/absence data, suggesting that patterns of biodiversity are more affected by changes in the relative abundance of dominant species rather than in faunal composition. Although the total pool of species available in gorgonian colonies appears to be the same in both sites analysed, each colony yields a rather small set of this species pool. All together the colonies may act as a metacommunity, but the structure of the assemblage in each colony (e.g. total number of species, dominance) apparently depends upon host attributes.

Keywords: biodiversity • β diversity • shallow water gorgonians • *Leptogorgia lusitanica* • *Eunicella gazella* • epibenthic assemblage structure • northeast Atlantic

3.1. Introduction

Coral habitats are one of the most diverse marine habitats (Knowlton et al., 2010), probably as a consequence of the complexity provided by their three-dimensional structure (Öhman and Rajasuriya, 1998; Gratwicke and Speight, 2005b; Idjadi and Edmunds, 2006; Lingo and Szedlmayer, 2006; Wilson et al., 2007) upon which several species depend, especially small invertebrates (Stella et al., 2010; Plaisance et al., 2011). These epifaunal organisms rely on coral colonies for food (e.g. Burkepile and Hay, 2007; García-Matucheski and Muniain, 2010) and protection against predators (e.g. Edwards and Emberton, 1980; Vytopil and Willis, 2001; Bergsma and Martinez, 2011), and may display several interactions with their hosts, including commensalism (Kumagai, 2008), predation (Burkepile and Hay, 2007; Schoepf et al., 2010; García-Matucheski and Muniain, 2010), symbiosis (Carricart-Ganivet et al., 2004; Stewart et al., 2006; Bergsma, 2010) and mutualism (Holbrook et al., 2008; Stachowicz and Hay, 1999; Bergsma and Martinez, 2011). Depending on the nature of the interaction, coral-associated invertebrates may provide sediment removal (Stewart et al., 2006), protection from predators (Pratchett, 2001; Stier et al., 2010), and ultimately contribute to enhance coral growth and survival (Bergsma and Martinez, 2011).

Studies on invertebrate species associated to coral reefs are relatively scarce, especially when compared to the knowledge on fish-associated assemblages, and most of them have been carried out in shallow-water Indo-Pacific regions (e.g. Coles, 1980; Edwards and Emberton, 1980; Patton, 1994; Goh et al., 1999; Vytopil and Willis, 2001; Kumagai and Aoki, 2003; Stella et al., 2010). To the authors' best knowledge, to date, only three quantitative studies on non-colonial invertebrate assemblages associated with corals were undertaken in cold-temperate Atlantic waters (Mortensen and Buhl-Mortensen, 2004; Buhl-Mortensen and Mortensen, 2005; Greene, 2008). However, research on the distribution patterns of coral species and associated fauna is required to better understand their role on coastal ecosystems and to develop sound scientific-based conservation measures aiming to regulate the sustainable use of these areas. Coral habitats considered as priority by OSPAR include coral gardens, *Lophelia pertusa* reefs and sea pen fields. Despite being one of the richest ecosystems on the planet, coral reefs are also among the most endangered, by pollution, destructive fishing practices and global climate change (Hoegh-Guldberg et al., 2007; Carpenter et al., 2008; Wilson et al., 2010). As expected, specialist species (those that depend on only one or two hosts) will be particularly susceptible to habitat degradation and loss (e.g. Munday, 2004). Therefore, a better understanding of the relationships between corals and associated organisms, such as small invertebrates, is also crucial for predicting potential biodiversity losses resulting from coral degradation. Currently, studies on coral-associated fish species revealed that declines in coral abundance resulted in corresponding decreases in fish abundance and diversity, with specialist species being more prone to extinction (Jones et al., 2004; Munday, 2004; Pratchett et al., 2011). In this particular, it is noteworthy that marine reserves might help to mitigate the

problem, but will not always be sufficient to reverse this negative pattern (Jones et al., 2004).

In marine systems, most studies of diversity change across spatial and temporal scales have been focused on local (α-) and regional (γ-) diversity, largely neglecting β-diversity (turnover or complementarity) (Gray, 2000; Becking et al., 2006). However, more recently, β-diversity has gained renewed interest and has been applied to gain further insights on the diversity patterns and processes underlying species dynamics at different spatial and temporal scales (e.g. Danovaro et al., 2009; Thrush et al., 2010; Dimitriadis and Koutsoubas, 2011; Bevilacqua et al., 2012), and thus pointed out as a valuable conservation tool (Gering et al., 2003). Facing the need for a better understanding of the relationships between corals and associated epifaunal assemblages, as well as the scarcity of data concerning cold-temperate octocoral reefs, the present study aims to describe the patterns of biodiversity, abundance and community structure of the epifaunal assemblages associated with shallow water gorgonians. The contribution of the inventory (α-diversity) and differentiation (β-diversity) components of diversity will be analysed across multiple scales of variability: host species, colony size, site location and time (inter-annual). The role of gorgonian gardens in promoting regional (γ-) diversity will be discussed. Therefore, in the present study we aim to answer the following questions: 1) will composition and structure of associated epifaunal assemblage vary with: i) colony size; ii) gorgonian host; 2) are these putative patterns in composition and structure consistent in: i) space; ii) time.

3.2. Materials and Methods

3.2.1. Studied species

The studied species, *Leptogorgia lusitanica* and *Eunicella gazella*, belong to two different genera with a worldwide distributional range. Although belonging to the family Gorgoniidae, *Leptogorgia lusitanica* and *Eunicella gazella* are morphologically different: *Leptogorgia lusitanica* colonies are generally larger in width than in height, while *Eunicella gazella* colonies are more evenly shaped (i.e. display similar width and height). *Leptogorgia lusitanica* colonies may reach up to 80 cm in width, while *Eunicella gazella* is a small-sized species reaching a maximum of 30 cm in height. Branches of *Leptogorgia lusitanica* may have different colours and are more flexible, while *Eunicella gazella* branches are generally thicker and white.

3.2.2. Sampling and laboratory procedures

Sampling was undertaken in two consecutive summers (2010 and 2011) at Pedra da Greta

(PG), the main rocky subtidal area in the central part of the Algarve coast, with approximately 3.6 km in length and ranging from 20 to 90 m in width. In PG, two sites (PG1 and PG2) located at approximately 15 m depth, were randomly selected to account for spatial variability. The summer period was chosen because it generally corresponds to the peak of invertebrates' diversity and abundance in this region.

Because of the variability in size of *Leptogorgia lusitanica* and *Eunicella gazella*, and to assess the influence of colony size in the biodiversity patterns, three size classes were previously established based on size frequency distributions of the two gorgonian species (Cúrdia et al., sub.a). For *Leptogorgia lusitanica* the size height ranges were: small, <10 cm; medium, 15–25 cm; large, >30 cm; whereas for *Eunicella gazella* the height ranges were: small, <8 cm; medium, 10–15 cm; large, >18 cm. At each site and sampling period, three replicates of each species and colony-size were collected by scuba diving (36 colonies per sampling occasion). The entire colony was enclosed in a plastic bag to prevent faunal loss and then carefully detached from the substrate. All gorgonians were transported to the laboratory for further processing.

In the laboratory, the colonies were preserved in 96 % ethanol. Samples were washed through a 100 µm mesh sieve and colonies were observed under a magnifying glass to ensure that all fauna (mobile and sessile epibionts) and flora had been removed. All specimens associated with each colony were preserved in 96 % ethanol and afterwards identified to the lowest practical taxonomic level. To estimate species richness, unidentifiable organisms were, whenever possible, differentiated into different operational taxonomic units (OTUs). If animals were juveniles and/or were extremely damaged, and it was impossible to recognize whether they were different entities or belong to any of the already identified species, they were excluded from the analyses. The abundance of macroscopic algae, cnidarians, bryozoans, sponges and hydrozoans was estimated by a semi-quantitative index ranging from 0 to 4, (0 – absent; 1 – rare; 2 – common; 3 – abundant; 4 – very abundant). This index will be the sum of the scores of each epibiont observed for each colony. In order to minimize bias, scoring was always performed by the same observer and for simplicity, this relative index will be hereafter designated as CEC (as for "colonial" epibiont cover, where the term colonial is used loosely to represent modular organisms). CEC will be used to infer the enhancement of functional intricacy of the gorgonian colonies derived from the presence of attached sessile organisms that may provide additional ecological niches and/or a greater variety of food resources for the attendant invertebrate assemblages. In the laboratory, the maximum height and width and the wet weight of each colony were measured (Table 3.1). Colony surface area was estimated using the image analysis software, ImageJ (Rasband, 2010), on digital photographs taken in the laboratory.

Table 3.1.: Mean (±SD) surface area (m^2), width (m) and height (m) of colonies sampled for both species. L – large; M – medium; S – small.

	Eunicella gazella			*Leptogorgia lusitanica*		
Size-class	**Area**	**Width**	**Height**	**Area**	**Width**	**Height**
L	6930 ± 2041.7	165.8 ± 27.7	201.1 ± 22.0	17410 ± 3908.9	375 ± 31.4	352 ± 56.2
M	4155 ± 1994.8	135.8 ± 34.3	145.8 ± 28.2	7041 ± 3082.5	241 ± 52.6	217 ± 46.7
S	1047 ± 350.7	76.2 ± 26.2	73.2 ± 13.0	1840 ± 976.0	133 ± 37.4	74 ± 16.8

3.3. Data analysis

Only taxa unambiguously assigned to different identities were considered and included in the analyses. The number of taxa, Shannon-Wiener diversity (H'), Pielou evenness index (J' Pielou, 1969) and Hurlbert (1971) expected species richness ($ES_{(n)}$) were calculated and used to describe patterns in biodiversity and to assess changes in community structure. Hurlbert's expected number of species, which can be rarefied to the same number of individuals (equal or lower than the lowest common number of individuals), is probably the most adequate estimate of biodiversity for the present study, because of the implications of size and shape on the total available area for colonization of each gorgonian colony. β-diversity was analysed in terms of complementarity (differences between colonies of different sizes, different species and different sites), and turnover (differences between consecutive years). In order to evaluate the level of dissimilarity in species composition and assemblage structure, we calculated the Bray-Curtis coefficients of dissimilarity based on the presence/absence and raw data matrices, respectively.

An analysis of similarities by randomization/permutation tests (ANOSIM) was performed on the samples grouped according to the relevant factors (colony size, host species, site and time). Specifically, four tests were undertaken. Test 1 was undertaken for factor "colony size" (3 levels: small, medium and large) separately for *Eunicella gazella* and *Leptogorgia lusitanica*. Test 2 was undertaken for factor "gorgonian host" (2 levels: *Eunicella gazella* and *Leptogorgia lusitanica*), aiming at assessing differences between sites and sampling years separately. Tests 3 and 4 were carried out for the evaluation of spatial (PG1 vs PG2) and temporal consistency (2010 vs 2011). Differences in epifaunal assemblage structure between gorgonian hosts, as well as the relationship between assemblage structure and habitat characteristics, were analysed by a distance-based redundancy analysis (dbRDA) (McArdle and Anderson, 2001). Size-related attributes of gorgonian colonies, such as total surface area, maximum width and height were used as habitat characteristics and CEC was also used as an additional attribute, because of its recognized role for the occurrence and abundance of mobile invertebrates (Guerra-García, 2001; Cacabelos et al., 2010). To analyse the contribution of each species to the discrimination of the epifaunal assemblages associated with both gorgonians, the indicator value (IndVal) was

used (Dufrêne and Legendre, 1997). Epifaunal species overlap and the existence of potential habitat-specialists was also analysed by comparing both datasets with and without singletons (i.e. taxon represented by a single organism or found on a single colony). Potential habitat-specialists are distinguished from rare taxa based on their frequency distribution across replicates of each gorgonian species (Stella et al., 2010). Indeed, taxa collected from only one of the hosts could either be: i) rare taxa that have a low rate of occurrence regardless of host; ii) species that do not use gorgonians as a preferred habitat and therefore are rarely found; or iii) habitat-specialists that only occur on certain hosts (Stella et al., 2010). Consequently, the occurrence rates were also evaluated when singletons were removed from the dataset (Stella et al., 2010). All statistical analyses were performed using the open source software R version 12.1 (R Development Core Team, 2010).

3.4. Results

A total of 181 taxa were identified from the 72 gorgonian colonies (*Eunicella gazella* – 124 taxa; *Leptogorgia lusitanica* – 144 taxa). These taxa were ascribed to 11 phyla, 15 classes, 41 orders, 99 families and 150 genera comprising a total of 7284 individuals. Overall, *Leptogorgia lusitanica* colonies had more taxa and harboured more individuals than those of *Eunicella gazella* (*Leptogorgia lusitanica* – 4382 individuals; *Eunicella gazella* – 2902 individuals). Regarding the taxonomic composition at the highest taxonomic level (phylum), the general pattern was very similar for both gorgonian species. Epifaunal assemblages associated with both gorgonians were numerically dominated by arthropods, accounting for up to 48 % and 65 % of total abundance in *Eunicella gazella* and *Leptogorgia lusitanica*, respectively. Molluscs were also abundant in both gorgonians (18 % in *Eunicella gazella* and 22 % in *Leptogorgia lusitanica*) and Platyhelminthes, which were exclusive of *Eunicella gazella* epifaunal assemblages, were the second most abundant group in this species. In terms of richness (i.e. the number of different OTUs), annelids (and especially polychaetes) were highly diverse (over 33 % of total species on both gorgonians).

3.4.1. Biodiversity patterns

The abundance (i.e. the number of individuals per colony) varied from 6 to 358 in *Eunicella gazella* and from 8 to 737 in *Leptogorgia lusitanica*. In 2010, the mean abundance of epifauna was higher in *Leptogorgia lusitanica* colonies (154.4±42.5 individuals) than in *Eunicella gazella* colonies (62.3±16.3 individuals), whereas in 2011 values were slightly higher in *Eunicella gazella* (98.9±19.2 individuals) than in *Leptogorgia lusitanica* (89.1±25.8 individuals) (Figure 3.1). The number of taxa per colony varied between 4 and 55 in *Eunicella gazella*, ranging form 5 to 63 in *Leptogorgia lusitanica*. Mean species richness per colony was consistently lower in *Eunicella*

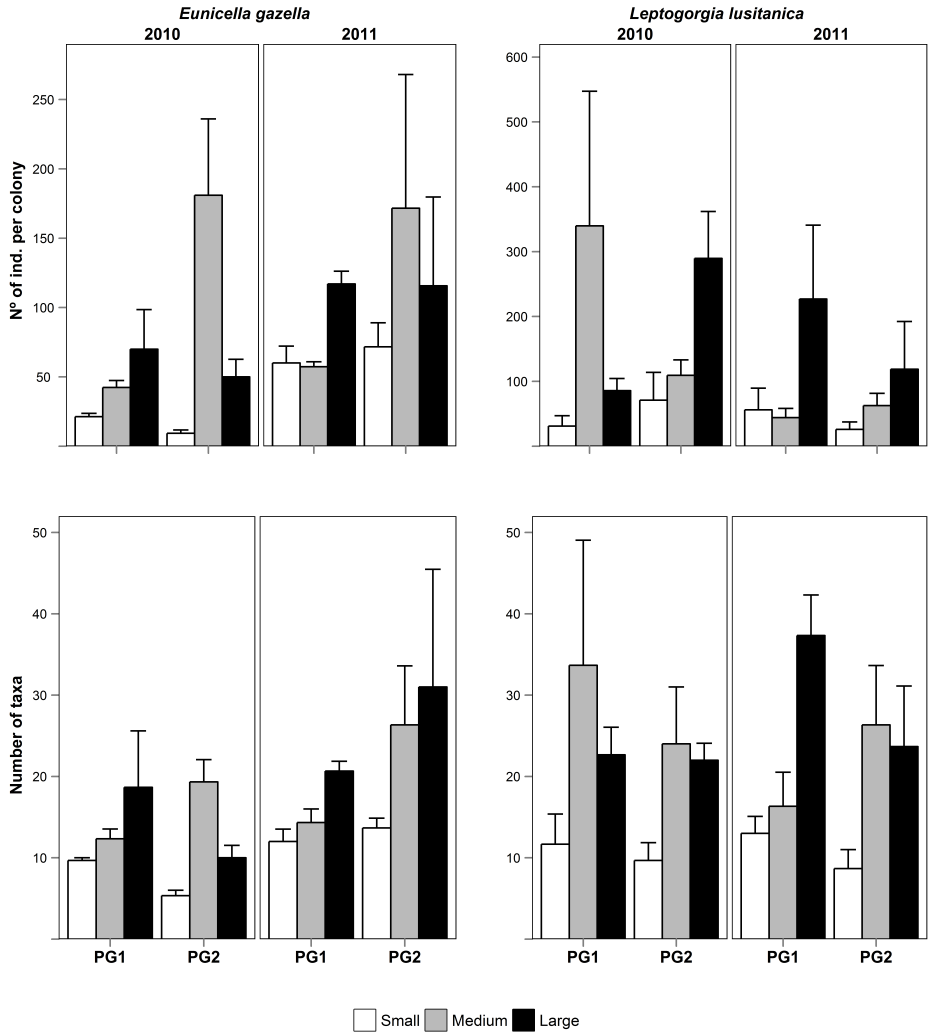

Figure 3.1.: Variation in the number of individuals and number of species per colony (+SE) of epifauna associated with *Eunicella gazella* and *Leptogorgia lusitanica* for both years, areas (PG1 and PG2) and according to colony size classes (small, medium and large).

gazella (2010, 12.6±1.6; 2011, 19.7±2.9, Figure 3.1) compared to *Leptogorgia lusitanica* (2010, 20.6±3.2; 2011, 20.9±2.9, Figure 3.1).

3.4.2. Effect of colony size

Hurlbert's $ES_{(100)}$ values ranged in *Eunicella gazella* from 19.8 (small-sized colonies in PG2) to 34.6 (large-sized colonies in PG2), while in *Leptogorgia lusitanica* values ranged from 18.4 (small-sized colonies in PG2) to 34.5 (medium-sized colonies in PG2) (Table 3.2). Minimum and maximum values were comparable for both gorgonians, but while in *Eunicella gazella* there

was a steady increase in the number of species with colony size, in *Leptogorgia lusitanica* this increase was abrupt from small to medium-sized colonies (Table 3.2). In both hosts, the number of individuals per colony was also lower in small than medium to large-sized colonies, but there was no clear pattern for J'. Large colonies of *Eunicella gazella* and medium colonies of *Leptogorgia lusitanica* (both in PG2) had the highest $ES_{(100)}$ and J' values and offered more redundancy to the overall biodiversity in terms of expected number of species (Figure 3.2 and Table 3.2). However, there was always some degree of complementarity in the assemblages of different colonies, as the pooled number of species for each colony size was always much lower than the grand total for each host species (Table 3.2). Although different in terms of species composition, small-sized colonies generally showed more similar values of N, S and $ES_{(100)}$ between gorgonian species than larger colonies (Table 3.2). The main differences for each gorgonian host were found between small colonies and the remaining size classes. ANOSIM analysis confirmed this trend, indicating that community structure and composition were significant different between small- and medium- to large-sized colonies but not between medium and large colonies (Table 3.3, Test 1).

Table 3.2.: Abundance and biodiversity data for *Eunicella gazella* (EG) and *Leptogorgia lusitanica* (LL) per colony size class (S - small; M - medium and L - large), site (PG1 and PG2) and year (2010 and 2011). n - number of colonies; N - number of individuals per colony; S - number of taxa per colony; $ES_{(100)}$ - Hurlbert's expected number of species per 100 individuals; H' - Shannon-Wiener diversity; J' - Pielou's evenness.

	n	N	S	$ES_{(100)}$	$H'_{\log_e}$	J'		n	N	S	$ES_{(100)}$	$H'_{\log_e}$	J'
EG S PG1	6	244	31	20.14	2.39	0.695	**LL S PG1**	6	261	35	23.57	2.76	0.776
EG S PG2	6	243	29	19.78	2.22	0.659	**LL S PG2**	6	291	28	18.40	2.48	0.744
EG M PG1	6	299	35	22.88	2.47	0.695	**LL M PG1**	6	1151	80	27.89	3.09	0.705
EG M PG2	6	1058	64	23.23	2.61	0.628	**LL M PG2**	6	516	74	34.48	3.33	0.774
EG L PG1	6	561	60	25.00	2.57	0.627	**LL L PG1**	6	938	84	30.48	3.20	0.721
EG L PG2	6	497	74	34.57	3.17	0.737	**LL L PG2**	6	1225	73	21.22	2.30	0.535
EG S	12	487	45	21.18	2.46	0.647	**LL S**	12	552	47	22.37	2.83	0.735
EG M	12	1357	74	24.17	2.71	0.629	**LL M**	12	1667	105	32.50	3.35	0.719
EG L	12	1058	99	32.11	3.03	0.659	**LL L**	12	2163	105	26.97	2.93	0.629
EG PG1	18	1104	77	24.84	2.66	0.613	**LL PG1**	18	2350	120	31.34	3.32	0.694
EG PG2	18	1798	102	28.98	2.94	0.636	**LL PG2**	18	2032	105	26.37	2.81	0.604
EG 2010	18	1122	67	24.22	2.79	0.665	**LL 2010**	18	2779	102	26.46	2.95	0.637
EG 2011	18	1780	99	27.48	2.76	0.602	**LL 2011**	18	1603	106	31.81	3.29	0.706
EG	36	2902	124	28.23	2.92	0.606	**LL**	36	4382	144	30.51	3.29	0.661
EG+LL 2010	36	3901	123	27.52	3.12	0.648	**EG+LL PG1**	36	3454	140	30.95	3.33	0.673
EG+LL 2011	36	3383	139	31.39	3.20	0.649	**EG+LL PG2**	36	3830	143	29.74	3.15	0.634
Total	72	7284	181	31.41	3.36	0.646							

3.4.3. Effect of gorgonian host

The epifaunal assemblage associated with *Eunicella gazella* usually showed much lower abundance than in the one associated with *Leptogorgia lusitanica* and often slightly lower values of the biodiversity indices both of α-diversity (S, ES_{100}, H'; Table 3.2) and β-diversity (average dissimilarity between colonies; Figure 3.3 B1, B2, C1 and C2). The variation in abundance and specific composition, leading to the differences observed in the community structure, can be illustrated by J' values; in general, evenness was higher in *Leptogorgia lusitanica* than in *Eunicella gazella* (Table 3.2). The higher dominance of the epifaunal assemblages associated with *Eunicella gazella* was also confirmed by the cumulative percentage of abundance of the three most abundant taxa (Table 3.4). Despite some rank shifts, in *Eunicella gazella* the same three taxa, *Erichthonius punctatus*, an undetermined species of Turbellaria and Ostracoda, shared consistently more than 50 % dominance irrespective to size, site or year, while in *Leptogorgia lusitanica* the first three ranks of dominance, accounting for 35 to 54 % dominance were shared by five different taxa (four amphipod species and Ostracoda), depending on colony size, site and year (Table 3.4). Differences between the assemblages associated with the two gorgonian hosts were always significant irrespective to site or year (ANOSIM Test 2, Table 3.3). The complementarity of the assemblages from *Eunicella gazella* and *Leptogorgia lusitanica* is shown by the comparison of the rarefaction curves for each gorgonian species and "Total" in Figure 3.2, but also by the high median dissimilarity between colonies when the estimates include comparisons between both hosts (Figure 3.3 A1 and A2).

Of the 181 OTUs identified, 48.1 % (87 species) were common to both gorgonian hosts, whereas 37 species (20.4 %) were exclusively found in *Eunicella gazella* colonies and 57 species (31.5 %) only occurred in *Leptogorgia lusitanica*. However, among those exclusive taxa, there were several singletons. Removing singletons from the analysis, the percentage of exclusive taxa dropped to a total of 16 % (corresponding to 29 taxa, 11 exclusive of *Eunicella gazella* and 18 exclusive of *Leptogorgia lusitanica*, Table 3.5). From these taxa, only the undetermined species of Turbellaria was frequent and abundant in *Eunicella gazella* colonies. Only five other taxa occurred in more than 10 % of the colonies, namely the bivalve *Glans* sp. in *Eunicella gazella* and Ophiuridae sp.B, and the polychaetes *Lumbrineris tetraura*, *Serpula vermicularis* and *Syllis* cf. *columbretensis* in *Leptogorgia lusitanica* (Table 3.5). The remaining taxa displayed either low abundance or frequency of occurrence (Table 3.5).

Table 3.3.: Results of the ANOSIM global and pairwise tests for *Eunicella gazella* (EG) and *Leptogorgia lusitanica* (LL), based on untransformed abundance data (raw) and presence/absence data (P/A). Significance tests (999 permutations) were performed for differences in colony size classes (S - small; M - medium and L - large), sites (PG1 and PG2) and sampling years (2010 and 2011). * - $p < 0.05$; ** - $p < 0.01$; *** - $p < 0.001$; ns - not significant

Source of variability		Raw	P/A
Test 1		R	R
Colony size			
Eunicella gazella			
	Global test	$0.150 * **$	$0.107 * **$
	Pair-wise tests		
	S, M	$0.153 * *$	$0.182 * **$
	S, L	$0.171 * *$	$0.161 * *$
	M, L	$-0.073 ns$	$-0.027 ns$
Leptogorgia lusitanica			
	Global test	$0.182 * **$	$0.241 * **$
	Pair-wise tests		
	S, M	$0.181 *$	$0.270 * **$
	S, L	$0.283 * *$	$0.453 * **$
	M, L	$-0.011 ns$	$-0.012 ns$
Test 2			
Gorgonian host			
	within site		
	PG1, EG vs LL	$0.507 * **$	$0.291 * **$
	PG2, EG vs LL	$0.355 * **$	$0.233 * **$
	within time		
	2010, EG vs LL	$0.390 * **$	$0.278 * **$
	2011, EG vs LL	$0.476 * **$	$0.223 * **$
Test 3			
Site			
	EG, PG1 vs PG2	$0.043 ns$	$0.018 ns$
	LL, PG1 vs PG2	$0.058 ns$	$-0.009 ns$
	PG1 vs PG2	$0.018 ns$	$0.004 ns$
Test 4			
Time			
	EG, 2010 vs 2011	$0.141 * *$	$0.253 * **$
	LL, 2010 vs 2011	$0.288 * **$	$0.187 * **$
	2010 vs 2011	$0.189 * **$	$0.222 * **$

Table 3.4.: First dominant species for *Eunicella gazella* (EG) and *Leptogorgia lusitanica* (LL) per colony size class (S - small; M - medium and L - large), site (PG1 and PG2) and year (2010 and 2011).%N - relative taxa abundance.

EG S	**%N**	**EG M**	**%N**	**EG L**	**%N**	**LL S**	**%N**	**LL M**	**%N**	**LL L**	**%N**
Erichthonius punctatus	29.8	*Erichthonius punctatus*	25.4	Turbellaria	32.9	*Caprella fretensis*	12.3	Ostracoda	15.5	*Caprella fretensis*	26.9
Turbellaria	22.6	Turbellaria	21.6	*Erichthonius punctatus*	9.7	*Gammaropsis* cf. *crenulata*	12.3	*Gammaropsis* cf. *crenulata*	12.5	Ostracoda	13.1
Ostracoda	8.2	Ostracoda	10.7	Ostracoda	8.8	Ostracoda	10.7	*Hiatella arctica*	8.5	*Erichthonius punctatus*	12.2
	60.6		**57.7**		**51.4**		**35.3**		**36.4**		**52.2**
EG PG1	**%N**	**EG PG2**	**%N**	**EG**	**%N**	**LL PG1**	**%N**	**LL PG2**	**%N**	**LL**	**%N**
Turbellaria	35.9	*Erichthonius punctatus*	25.4	Turbellaria	25.9	Ostracoda	15.0	*Caprella fretensis*	33.8	*Caprella fretensis*	16.0
Erichthonius punctatus	12.4	Turbellaria	19.7	*Erichthonius punctatus*	20.4	*Gammaropsis* cf. *crenulata*	12.2	Ostracoda	12.2	Ostracoda	13.7
Ostracoda	7.8	Ostracoda	10.7	Ostracoda	9.6	*Erichthonius punctatus*	8.4	*Erichthonius punctatus*	8.1	*Erichthonius punctatus*	8.3
	56.1		**55.8**		**55.9**		**35.7**		**54.1**		**37.9**
EG 2010	**%N**	**EG 2011**	**%N**	**EG +LL 2010**	**%N**	**LL 2010**	**%N**	**LL 2011**	**%N**	**EG + LL 2011**	**%N**
Turbellaria	24.2	Turbellaria	26.9	*Caprella fretensis*	17.4	*Caprella fretensis*	24.3	*Erichthonius punctatus*	19.8	*Erichthonius punctatus*	23.4
Ostracoda	15.4	*Erichthonius punctatus*	26.6	Ostracoda	15.6	Ostracoda	15.7	Ostracoda	10.3	Turbellaria	14.2
Erichthonius punctatus	10.7	Ostracoda	5.9	*Gammaropsis* cf. *crenulata*	7.0	*Gammaropsis* cf. *crenulata*	8.6	*Gammaropsis* cf. *crenulata*	7.1	Ostracoda	8.0
	50.4		**59.4**		**40.0**		**48.5**		**37.2**		**45.5**

The dbRDA indicated that the first two ordination axes explain 84 % of the fitted variation (explained size-related attributes and CEC) comprising about 16 % of the total variation. The ordination plot also revealed a general separation of the epifaunal assemblages associated with the two gorgonian species (along the YY axis, CAP2). The length of the vectors also indicates that size-related attributes of the hosts were relevant for this discrimination. The Turbellaria undetermined species (absent from *Leptogorgia lusitanica* colonies) was responsible for the separation between gorgonian species, while the remaining taxa were much more abundant in *Leptogorgia lusitanica* colonies (Figure 3.4). Indeed, the IndVal identified Turbellaria as the only taxon with a significant association with *Eunicella gazella* (IndVal = 0.986, $p < 0.001$). On the other hand, the molluscs *Simnia spelta* (IndVal = 0.850, $p < 0.001$) and *Tritonia* sp. (IndVal = 0.757, $p < 0.01$), the crustaceans Astacilla sp. (IndVal = 0.773, $p < 0.001$), *Caprella fretensis* (IndVal = 0.723, $p < 0.001$), *Janira maculosa* (IndVal = 0.590, $p < 0.01$) and *Stenothoe* cf. *cavimana* (IndVal = 0.543, $p < 0.05$), as well as the anemone *Corynactis viridis* (IndVal = 0.657, $p < 0.01$) were all significantly associated with *Leptogorgia lusitanica*.

3.4.4. Spatial and temporal patterns

Despite all the variability found in the attendant assemblages depending on gorgonian colony size or host species, these effects do not translate into a significant spatial effect between sites (ANOSIM Test 3, Table 3.3).

Differences in the attendant epifaunal assemblages between years were always highly significant either considering each species separately or both species together (ANOSIM Test 4, Table 3.3). In opposition to the observations related to location, there was a change in the total pool of species of the two consecutive years. Turnover was always above 60 % (either considering each species separately or both species together) and resulted mostly from replacement of rare species but also from changes in the dominant species, especially in the epifaunal assemblage of *Leptogorgia lusitanica* (Table 3.4). An increase in α-diversity (S, $ES_{(100)}$) was also observed in 2011, but although the highest increase in number of species was observed in *Eunicella gazella* it was the increase in evenness of the *Leptogorgia lusitanica* assemblages (accompanied by a decrease in abundance) that contributed the most to the higher values of $ES_{(100)}$ in 2011 (Table 3.2 and Figure 3.2). In fact, the rarefaction curves for LL2011, EG+LL2011 and Total (Figure 3.2 D) show almost complete overlap. On the other hand, in general, β-diversity was lower in 2011 (Figure 3.3), with the decrease in median dissimilarity more accentuated in the *Eunicella gazella* assemblage (Figure 3.3 C1 and C2).

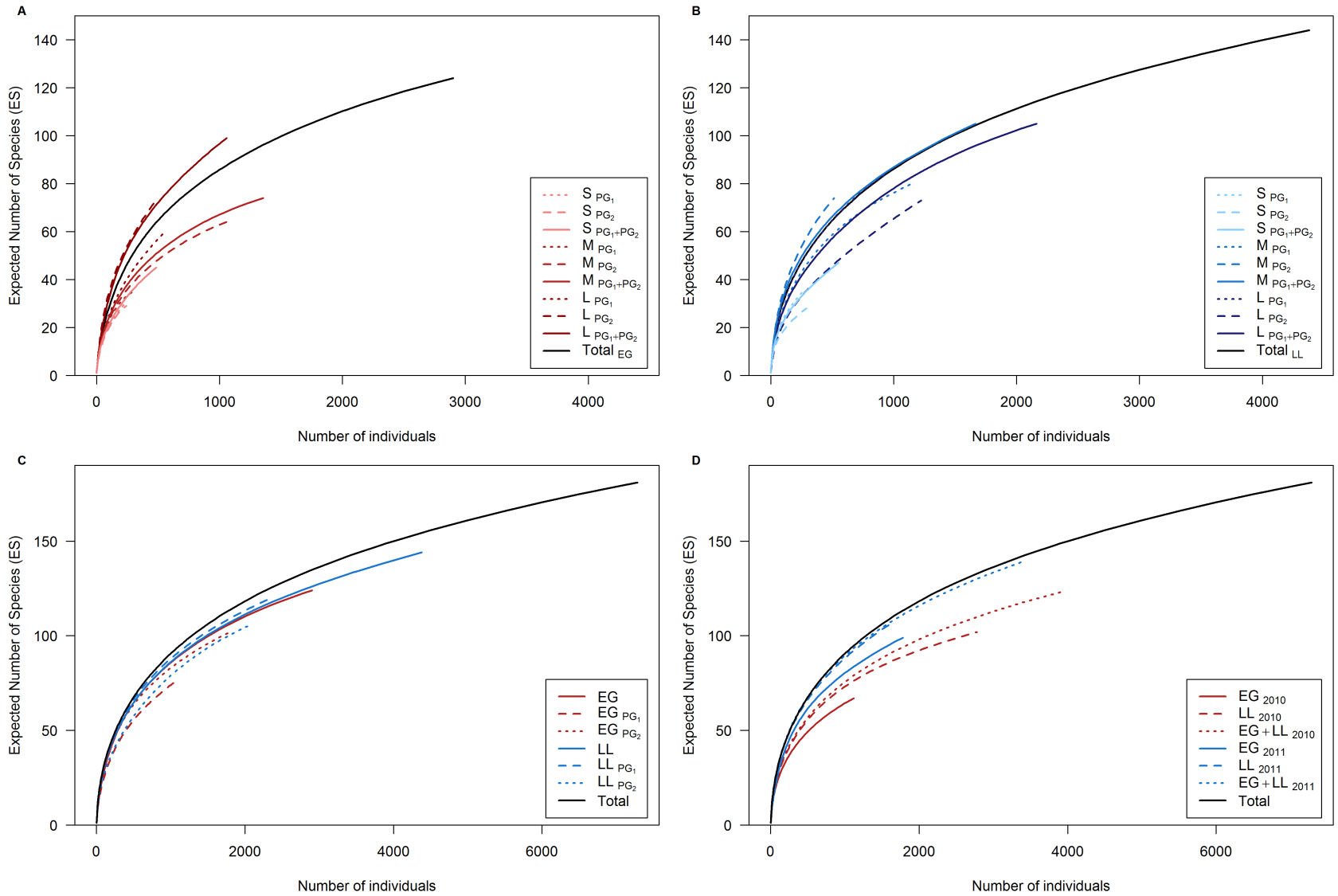

Figure 3.2.: Comparison of rarefaction curves (Hurlbert's expected number of species) for different colony sizes in (a) *Eunicella gazella* and (b) *Leptogorgia lusitanica* and for (c) spatial and (d) temporal scales. S - small; M - medium; L - large; PG1 and PG2, two sampling sites.

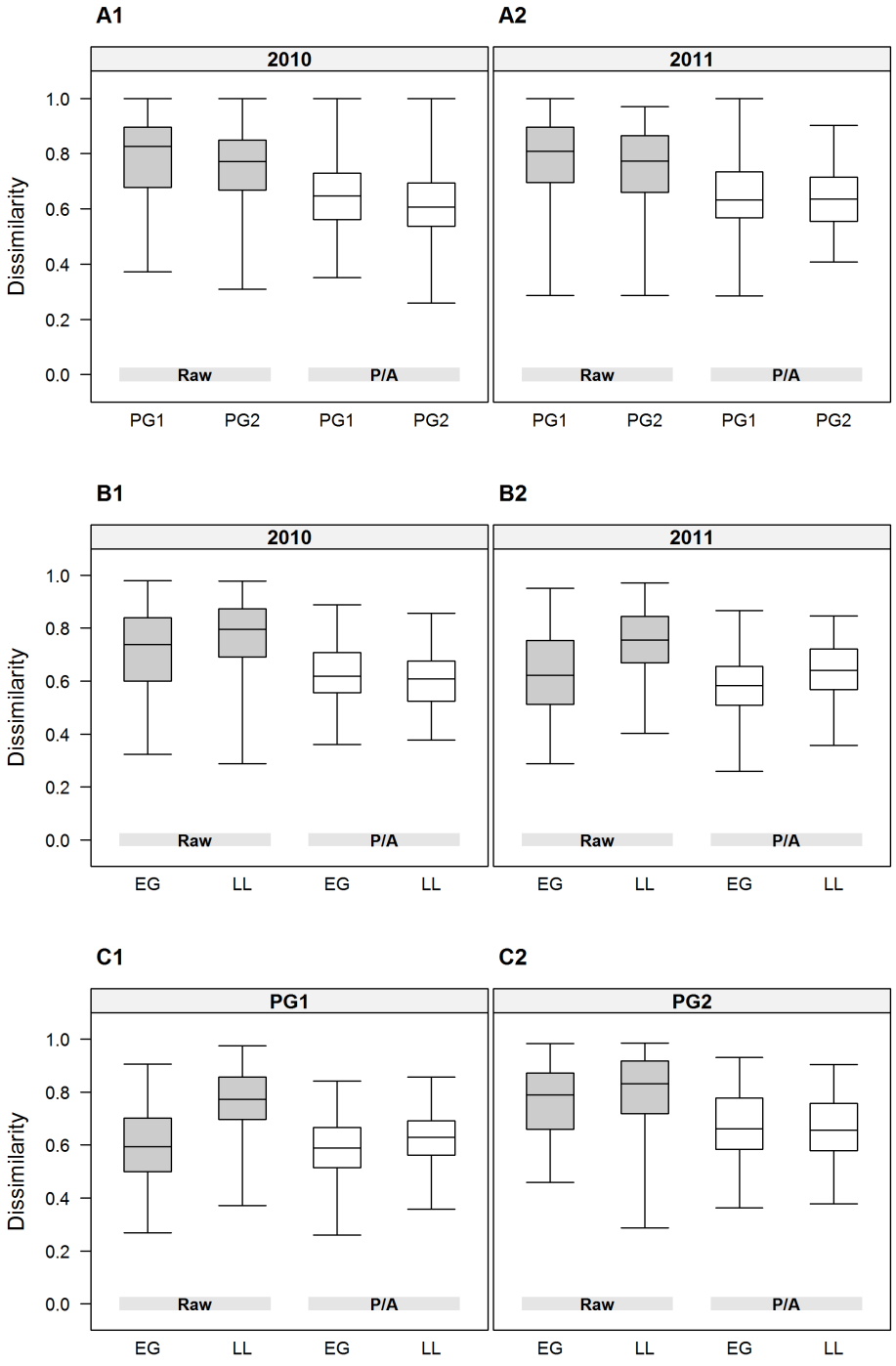

Figure 3.3.: Boxplots showing the median, inter-quartiles (box) and minimum and maximum values (whiskers) of Bray-Curtis coefficients of dissimilarity based on raw and presence/absence data for comparisons of β-diversity patterns analysed in terms of differences between gorgonian hosts for each year and site (A1, A2), differences between sites for each year and host (B1, B2) and differences between years for each site and host (C1, C2) (n=153). EG, *Eunicella gazella*; LL, *Leptogorgia lusitanica*.

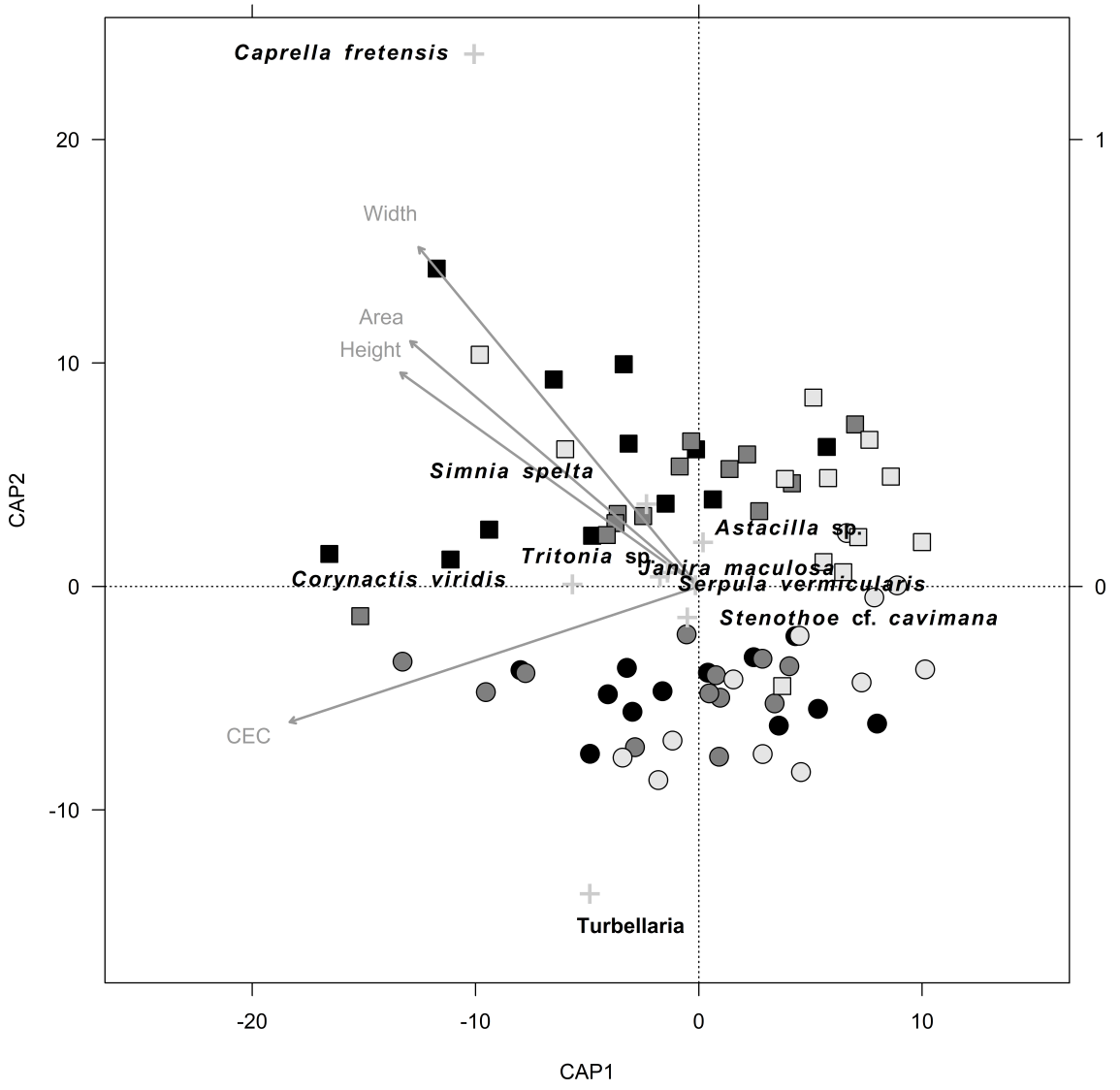

Figure 3.4.: Distance based Redundancy analysis (dbRDA) ordination triplot for epifaunal species. Circles (*Eunicella gazella*) and squares (*Leptogorgia lusitanica*) represent the samples (each colony sampled) position within the ordination space. The vector lines reflect the relationship of gorgonians' morphometric attributes (total area, width and height) and abundance of colonial epibiota to the ordination axes; their length is proportional to their relative significance. Only taxa identified by the indicator value (IndVal) as significantly contributing to the discrimination of both gorgonian species were included in the plot.

In both gorgonians, complementarity was higher when considering the raw abundance data when compared to the presence/absence matrix (Figure 3.3). This was also observed for differences between gorgonian hosts, indicating that community structure (relative abundance) rather than species composition had a higher contribution to patterns of complementarity.

Table 3.5.: Total abundance (N) and frequency of occurrence (F – % of colonies) of exclusive taxa to each one of the gorgonian species (without singletons).

Eunicella gazella				***Leptogorgia lusitanica***			
Phylum	**Taxa**	**N**	**F**	**Phylum**	**Taxa**	**N**	**F**
Annelida	cf. *Megalomma* sp.	2	5.6	Annelida	Acrocirridae sp.	2	5.6
Annelida	*Filograna implexa*	9	8.3	Annelida	*Ceratonereis costae*	2	5.6
Annelida	*Pseudosyllis brevipennis*	3	5.6	Annelida	Cirratulidae	2	5.6
Annelida	Terebellidae	2	5.6	Annelida	*Demonax thomasi*	5	8.3
Arthropoda	*Anoplodactylus pygmaeus*	2	5.6	Annelida	*Eunice* sp. B	2	5.6
Arthropoda	Lysianassidae sp.	3	8.3	Annelida	*Lumbrineris tetraura*	7	13.9
Mollusca	*Glans* sp.	4	11.1	Annelida	*Serpula vermicularis*	5	13.9
Mollusca	*Loripes* sp.	2	5.6	Annelida	*Syllis* cf. *columbritensis*	5	13.9
Mollusca	Nudibranchia sp. D	2	5.6	Annelida	*Ophryotrocha labronica*	4	8.3
Mollusca	Rissoidae	3	5.6	Arthropoda	*Apherusa bispinosa*	3	8.3
Platyhelminthes	Turbellaria	751	97.2	Arthropoda	*Jassa* sp.	2	5.6
				Arthropoda	*Palaemonetes varians*	4	8.3
				Chordata	Ascideacea sp. A	26	5.6
				Echinodermata	cf. *Genocidaris* sp.	3	5.6
				Echinodermata	Ophiuridae sp. B	7	11.1
				Mollusca	Phanerobranchia	2	5.6
				Mollusca	Bivalvia sp. C	2	5.6
				Mollusca	*Calliostoma zizyphinum*	2	5.6

3.5. Discussion

Epifaunal assemblages associated with the gorgonians *Leptogorgia lusitanica* and *Eunicella gazella* from shallow North Atlantic waters were rich (181 taxa) and abundant (7284 individuals). Eleven phyla were identified in the branches and upper basis of just two gorgonian species (36 colonies each). From the literature available (Table 3.6), values observed in the current study are comparable to the ones reported by Stella et al. (2010) within the branches of four scleractinian corals (12 phyla, 178 nominal species) in the Lizard Island (Great Barrier Reef, Australia), and much larger than those found by Goh et al. (1999) and Kumagai and Aoki (2003) in shallow water gorgonians' from Singapore (seven phyla) and Japan (five phyla), respectively (Table 3.6). A single gorgonian colony of *Leptogorgia lusitanica*, approximately 23 cm width, harboured more than 730 individuals from 63 species. The maximum abundance in *Eunicella gazella* (358 individuals) was recorded in a colony of approximately 11 cm width, while the peak of diversity (55 species) was registered in a larger colony measuring 23.6 cm width. Overall, the abundance values observed

in the present study are almost three times the values reported by Stella et al. (2010), although mesh-sieves are not comparable. It is expected that using a sieve with a larger mesh, abundance would be lower, but this was not observed in faunal assemblages associated with *Leptogorgia hebes*, *Leptogorgia virgulata*, and *Titanideum frauenfeldii* in shallow Atlantic waters from the coast of Georgia (Greene, 2008). In that study, 15 gorgonian colonies harboured over 56 000 individuals from 11 phyla (Table 3.6). Therefore, it is evident that shallow cold-temperate water gorgonians are relevant for the enhancement of local diversity and abundance of invertebrates, reinforcing the need for their conservation. Amongst the few quantitative studies on the relationship between coral reef communities and associated-invertebrates, Idjadi and Edmunds (2006) found that in the Caribbean reefs, scleractinian traits (namely, coral diversity, percentage cover of live coral, and the topographic complexity created by coral skeletons) were positively related with the diversity of reef-associated invertebrates. Besides, the enhancement of biodiversity is not restricted to the coral skeleton area, as it may be extended to the surrounding sediments (Cerrano et al., 2009).

The epifaunal assemblages of both gorgonian species were numerically dominated by arthropods, whereas in terms of diversity, annelids (especially polychaetes) were the richest group in *Eunicella gazella* colonies. Among arthropods, amphipods were the dominant taxa in both gorgonians contributing for a considerable proportion of total epifauna (37 % for *Eunicella gazella* and 46 % for *Leptogorgia lusitanica*). The dominance of amphipod species among crustacean fauna associated with gorgonians had also been reported for shallow (Greene, 2008) and deep (Mortensen and Buhl-Mortensen, 2004) Atlantic waters, as well as for shallow waters from the Indo-Pacific region (Goh et al., 1999; Kumagai and Aoki, 2003). In general, the composition of amphipod fauna was very similar (especially at family and genus level) to the reported for other Atlantic areas (Mortensen and Buhl-Mortensen, 2004; Greene, 2008), with the dominance of Caprellidae (*Caprella*), Ischyroceridae (*Erichthonius*, *Ischyrocerus* and *Jassa*), Photidae (*Gammaropsis* and *Photis*) and Stenothoidae (*Stenothoe*, in the present study; *Metopa* in deep-water gorgonians). The specimens of the genus *Caprella*, *Stenothoe*, *Erichthonius* and *Jassa* were also among the dominant fauna of artificial reefs in the Algarve region (Moura et al., 2007, 2008). On the other hand, the dominance of the genus *Caprella* in association with gorgonians had also been reported for Indo-Pacific shallow waters (Kumagai and Aoki, 2003), where gorgonian mortality has been reported related to a massive attack by caprellids (*Metaprotella sandalensis*) (Scinto et al., 2008).

Although considerably abundant among scleractinian coral hosts (e.g. Stella et al., 2010), amphipods are not dominant, being replaced by decapods (Table 3.6). Therefore, a consistent trend seems to emerge from the compilation of these studies indicating a dominance of amphipods among octocorals, whereas decapods dominate among hexacoral hosts (Table 3.6). Further investigation is, however, needed to confirm this trend, as studies are still scarce and differed on sampling procedures. A probable reason for this pattern is the higher availability of refuges

provided by sceleractian corals when compared to gorgonians, as it is known that crabs benefit from their association with corals by gaining refuge from predators (e.g. Stachowicz and Hay, 1999; Vytopil and Willis, 2001). This supports the earlier findings of Edwards and Emberton (1980) that reported the negative correlation between increased branching openness and decreased numbers of decapods in epifaunal assemblages associated with *Stylophora pistillata* (scleractinian), while Vytopil and Willis (2001) also suggested that branch tightness contributes to the protection of associated epifauna. The diversity of annelids assemblage associated with both gorgonians is by far higher than the reported by Goh et al. (1999) for shallow gorgonians from Singapore. On the other hand, based on studies performed for other coral groups, it seems that diversity of polychaetes is probably higher within gorgonians than among scleractinian species (e.g. Stella et al., 2010). Once more this needs confirmation as it can result from sampling bias.

3.5.1. Host attributes and associated biodiversity patterns

Non-colonial invertebrates were observed in all colonies sampled and, in general, *Leptogorgia lusitanica* harboured richer and more abundant assemblages, which can be at least partially explained by the resulting greater colonisable area of their colonies. Based on our results, colony size and time rather than location were the main drivers of variability in the attendant assemblages of the two gorgonian species. Increasing colony size translates directly into an increasing colonisable area, and, consequently, into a species-area effect, while inter-annual differences may reflect the dynamics of species life cycles (e.g. availability of recruits, success of recruitment), the response of individual species to environmental variability and at least partially a random drift in the composition of the assemblages from one year to another.

Table 3.6.: Quantitative studies on non-colonial invertebrate fauna associated with coral skeletons. shallow, <30 m; deep, >50 m; NDT - numerically dominant taxon

Coral type	Area	No. samples	Sieve	Depth level	No. phyla	No. taxa	No. ind.	NDT	Reference
Alcyonacea	Atlantic	72	100 µm	shallow	11	181	7284	amphipods	current study
Alcyonacea	Indo-Pacific	1600	500 µm	shallow	5	16		amphipods	Kumagai and Aoki, 2003
Alcyonacea	Indo-Pacific	NA	NA	shallow	7	30	NA	—	Goh et al., 1999
Alcyonacea	Atlantic	15	250 µm	deep	[a]	20	1540	amphipods	Mortensen and Buhl-Mortensen, 2004
Alcyonacea	Atlantic	25	250 µm	deep	9	114[c]	3915	crustaceans	Buhl-Mortensen and Mortensen, 2005
Alcyonacea	Atlantic	15	500 µm	shallow	11	NA	56751	amphipods	Greene, 2008
Scleractinian	Indo-Pacific	155	NA	shallow	[a]	49	NA	decapods	Edwards and Emberton, 1980
Scleractinian	Indo-Pacific	141	1000 µm	shallow	[b]	29	NA	decapods	Patton, 1994
Scleractinian	Indo-Pacific	48	1000 µm	shallow	3	NA	NA	decapods	Vytopil and Willis, 2001
Scleractinian	Indo-Pacific	200	1000 µm	shallow	12	178	2481	decapods	Stella et al., 2010

[a] crustaceans only; [b] decapods only; [c] colonial and non-colonial fauna; NA – data not available.

Although live surface area of corals was found to have no correlation either with abundance or species richness in *Acropora* colonies (Vytopil and Willis, 2001), the dbRDA analysis indicated strong relationships of size-related attributes (surface area, maximum width and height) and *Leptogorgia lusitanica* epifaunal assemblages. For both gorgonian species, small-sized colonies contributed the least for the overall biodiversity and showed significantly different epifaunal assemblages compared to medium- and large-sized colonies, confirming the relevance of colony size to biodiversity patterns in gorgonian gardens.

The colonial epibiont cover (e.g. macroscopic algae, sponges, bryozoans) was also observed to be determinant in structuring epifaunal assemblages of both gorgonian species. It is known that some of the dominant epifaunal taxa, such as caprellid amphipods, may also be closely associated with some of these colonial epizoans (e.g. briozoans, hydroids) (Aoki and Kikuchi, 1990; Guerra-García, 2001). Therefore, it is difficult to discern whether their abundance is due to the gorgonian itself or to the associated colonial organisms. The results of the dbRDA analysis supported the existence of a different structure in the epifaunal assemblage of the two gorgonian species. A single taxon (Turbellaria) was significantly associated with *Eunicella gazella* colonies, clearly resulting from its exclusivity to this host and its abundance and frequency of occurrence. On the other hand, seven taxa, although not exclusive, were indicated as significantly associated with *Leptogorgia lusitanica* colonies. These taxa were two gastropods (*Simnia spelta* and *Tritonia* sp.), four crustaceans (*Astacilla* sp., *Caprella fretensis*, *Janira maculosa* and *Stenothoe* cf. *cavimana*), and one cnidarian *Corynactis viridis*. *Simnia spelta*, *Tritonia* sp. and *Corynactis viridis* had already been reported as associated with gorgonians (Patton, 1972; Goh et al., 1999; Rodrigues, 2008; García-Matucheski and Muniain, 2010). Although both gorgonians shared most of the species collected, 11 and 18 taxa were exclusively associated with *Eunicella gazella* and *Leptogorgia lusitanica*, respectively (without considering singletons), supporting the existence of specificity of some taxa probably because of morphological differences between gorgonian species. Nevertheless, most of these exclusive taxa presented either low abundance or low frequency. The exception was one undetermined species of Turbellaria occurring in *Eunicella gazella* colonies. These white flatworms, which colour resembles the colour of *Eunicella gazella* branches, may take advantage of crypsis (Goh et al., 1999). We hypothesize that this specificity may reflect a strategy to avoid predation. Besides Turbellaria, only six amongst the exclusive taxa observed in each species showed a frequency of occurrence over 10 %: the bivalve *Glans* sp. in *Eunicella gazella*; the polychaetes *Lumbrineris tetraura*, *Serpula vermicularis* and *Syllis* cf. *columbretensis* and Ophiuridae sp.B in *Leptogorgia lusitanica*. *Serpula vermicularis* was already found within dead coral colonies and rocky substrates in deep Mediterranean waters (Mastrototaro et al., 2010), while *Lumbrineris tetraura* has been associated with soft (Bone and Klein, 2000) and hard (Giangrande et al., 2003) bottoms, as well as within seagrass meadows (Gambi et al., 1998). *Serpula vermicularis* has been frequently observed in hard bottoms from southern Portugal, particularly in artificial reefs (Moura et al., 2007, 2008), where *L. tetraura* and *Syllis* cf. *columbretensis* can also be less frequently found and presenting low

abundance (unpubl. data). On the other hand, the bivalves from genus *Glans* had been identified from fishing trawling samples in the study area (Malaquias et al., 2006). Therefore, these taxa cannot be considered gorgonian-obligate.

Currently, over 860 invertebrate species were described as being associated with coral species; at least half of them appear to have an obligate dependence on live corals and several species show a high degree of preference for one or two coral species (see Stella et al., 2010, for a review). Further research is needed, as these obligate associations and habitat specialization may contribute to a greater risk of extinction of associated invertebrates, especially taking into account the current scenario of ongoing degradation of coral habitats (Stella et al., 2010). Disregarding the level of dependence on the coral host, all taxonomic components symbiotic assemblages should be considered, as all have the capacity to contribute to the functioning of coral habitats (Gates and Ainsworth, 2011).

3.5.2. Biodiversity patterns: implications for future studies

Overall, the gorgonian species analysed in the present study appear to conform to the general paradigm that corals (generally for scleractinian corals) are habitats of enhanced abundance and biodiversity. Therefore, gorgonians, as foundation species (Roff and Zacharias, 2011) in the marine environment, promote the existence of a wide diversity of species which may reflect the multiple microhabitats available within each colony (Buhl-Mortensen and Mortensen, 2005). Our results show not only the high values of α-diversity in the epifaunal assemblages associated with the gorgonian hosts but also intricate patterns of variability in the composition and structure of these assemblages leading to high values of β-diversity. The analysis of α-diversity showed the complementarity between individual colonies of different sizes and between colonies of different host species as well as an important inter-annual turnover in the attendant assemblages. Each individual colony encloses a small and highly variable subset of the total pool of species. The aggregation of colonies facilitates a metacommunity dynamics for which random drift of individuals between colonies may have a strong contribution and explains the lack of significant spatial variation at the local level. In a metacommunity dynamic resulting from ecological connectivity (Leibold et al., 2004), patterns of biodiversity are more affected by changes in the relative abundance of dominant species rather than in faunal composition. On the other hand, some characteristics of the attendant assemblages appear to be driven or at least affected by the attributes of their hosts. The host species may be relevant in attracting preferentially some attendant species and somehow also determine dominance patterns while colony size has a significant effect on the abundance and number of species of the attendant assemblage. Also, a high turnover in these epifaunal assemblages was observed and we hypothesize that this temporal fluidity in composition and structure are related to multiple factors including not only a

component of stochasticity but also life history events and response to environmental variability.

3.5.3. Final remarks

Besides being scarce, studies on the coral-associated epifaunal assemblages do not usually assess the β-diversity component and, consequently, are of limited use for comparisons with the present study. Our observations have important implications for the design of future biodiversity assessment studies, highlighting the need to take into account not only α- but also β-diversity (both complementarity and turnover) for an accurate perception of the habitat and its dynamics. More than focusing on a single gorgonian species, conservation efforts should be placed on the whole habitat encompassing different hosts and the size structure of their populations. Our findings support the recent proposal of "coral gardens" in south Portugal and Spain for the OSPAR list of protected habitats (Convention for the Protection of the Marine Environment of the North-East Atlantic) (Anonymous, 2011).

Acknowledgements

S.C. (SFRH/BPD/26986/2006) benefits from a post-Doctoral grant awarded by "Fundação para a Ciência e a Tecnologia" (FCT)'. J.C. (SFRH/BD/29491/2006) benefits from a PhD grant from the "Fundação para a Ciência e a Tecnologia" (FCT)'.

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CHAPTER 4

Diversity and abundance of invertebrate epifaunal assemblages associated with gorgonians are driven by colony attributes

Submitted to: *Coral Reefs*

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Abstract

Coral reefs and aggregations are generally recognized among the richest marine habitats but, there are only a few quantitative studies describing the relationships between corals' attributes and their associated epifaunal assemblages. The present study constitutes the first attempt to explicitly quantify the link between gorgonians (Octocorallia: Alcyonacea) and the abundance and species richness of associated non-colonial epifaunal invertebrates. These community descriptors showed a significant correlation to the measured colony attributes of the gorgonians *Leptogorgia lusitanica* and *Eunicella gazella*, namely the surface available for colonization (colony height, width and area), complexity and heterogeneity (fractal dimension and lacunarity respectively) and "colonial" epibiont cover (colonial fauna and macroscopic algae). The results highlight the variation in epifaunal assemblage response to gorgonian colony characteristics, even when these are closely related and share similar evolutive histories, like in the present case. The nature and intensity of the relationships were not only gorgonian species-dependent but varied from one taxonomic group to another. In all faunal groups associated with the two gorgonian species analysed, the species richness and abundance were strongly correlated with "colonial" epibiont cover. In fact, colonial epibiont cover possibly due to a trophic effect (direct or indirect enhancement of food availability) combined with the surface available for colonization (species-area effect) were the strongest predictors of species richness and abundance. On the other hand, although structural complexity is usually indicated as the main driver for the rich and abundant coral-associated assemblages, fractal dimension and heterogeneity were only relevant for the assemblages associated with *Leptogorgia lusitanica*. The validity of the paradigm that structural complexity enhances biodiversity may be scale-dependent. In the case of gorgonians, the effect of complexity at the "garden" level may be much more relevant than at the individual colony level reinforcing the need for the conservation of gorgonian aggregation areas as a whole in order to preserve host diversity and size structure.

Keywords: gorgonians • invertebrate biodiversity • structural complexity • fractal dimension • lacunarity • multiple regression

4.1. Introduction

A likely mechanism by which marine habitats might influence associated animal assemblages is through provision of complex habitats; in general structurally complex marine habitats (e.g. sponge and octocoral aggregations, coral reefs) support a greater number of species than simple ones (e.g. Gratwicke and Speight, 2005b). A wider range of niche availability (Attrill et al.,

1996; Kovalenko et al., 2012), refuge against predators (Jordan et al., 1996; Vytopil and Willis, 2001; Gratwicke and Speight, 2005a; Lingo and Szedlmayer, 2006) and increased availability of colonizable surface translated in a species-area relationship (Dean and Connell, 1987; Attrill et al., 2000, but see Matias et al., 2010) have been suggested as potential explanations for the higher biodiversity of complex systems. Testing the role of habitat complexity rigorously is difficult because of the lack of a widely accepted and objective measure of habitat complexity (Parker et al., 2001) but several proxies have been applied to coral reef areas: surface topography of the bottom (Öhman and Rajasuriya, 1998), visual estimation of habitat topography (encompassing reef topography, reef height, rugosity and number of refuge cavities; Wilson et al. 2007), cover of branching coral colonies (Chabanet et al., 1997), acoustic roughness (Bejarano et al., 2011), habitat assessment score (integrating rugosity, variety of growth forms, height, refuge size categories, percentage live cover and percentage hard substratum; Gratwicke and Speight 2005b), and fractal dimension (Bradbury and Reichelt, 1983; Knudby and LeDrew, 2007; Zawada et al., 2010). At the scale of the individual colony, fractal dimension has also been applied to quantify coral shape (Martin-Garin et al., 2007), morphological variability (Kruszyński et al., 2007) or even for modelling coral growth (Merks et al., 2003). Measurement of fractal dimension (*D*) allows obtaining a formal estimate of a habitat's physical complexity regardless the specific structural components (Beck, 2000).

The biodiversity of coral habitats is dominated by invertebrates that rely on corals for food, shelter or settlement cues (see Stella et al., 2011, for a review). Because of their mainly sedentary behaviour or reduced mobility, small invertebrates are expected to have stronger relationships with habitat characteristics (shape, niche availability, complexity) than fish and, consequently, are potentially more susceptible to habitat change (Stella et al., 2010). The role of coral host attributes in structuring associated invertebrates' assemblages have been assessed for the hexacorals *Pocillopora* and *Acropora* (Vytopil and Willis, 2001; Stella et al., 2010, and references therein) but not for octocoral species, such as gorgonians. Although most studies indicate a relationship between epifaunal abundance and species richness and the habitat structure of coral colonies (Abele and Patton, 1976; Coles, 1980; Julian Caley et al., 2001; Vytopil and Willis, 2001; Stella et al., 2010) results were not consistent. Although a few studies focusing on invertebrate fauna associated with gorgonians (Octocorallia: Alcyonacea) were already undertaken, little information is available, especially in shallow temperate Atlantic waters, about the actual contribution of gorgonians to local biodiversity, and in what extent gorgonian attributes affects this relationship. As other corals, gorgonians have been pointed out as foundational species in the sense that they maintain a high biodiversity of their attendant assemblages both at the aggregation and at the individual colony levels, namely by providing a great variety of niches, ranging from sheltered cavities to high water-flow areas with little sedimentation (Buhl-Mortensen and Mortensen, 2005).

"Coral gardens" (mainly gorgonian aggregations) are frequent in NE Atlantic and Mediter-

ranean Sea (Gori et al., 2011a) and were recently proposed for the OSPAR (Convention for the Protection of the marine Environment of the North-East Atlantic) list of protected habitats (Anonymous, 2011), because of their vulnerability and high conservation value. In a previous study we demonstrated the high biodiversity associated with gorgonian gardens in the south of Portugal (Carvalho et al., sub.). Herein we provide the first quantitative data on the relationship and consistency between the abundance and biodiversity of the attendant epifaunal assemblages and a set of gorgonian colony attributes intended to represent the effects of the surface available for colonization, the structural complexity and heterogeneity, and the functional (trophic) intricacy. In previous studies namely on epifaunal assemblages associated with seagrasses and macroalgae, epiphytes were found to have a relevant role in structuring associated mobile epifaunal assemblages (Cacabelos et al., 2010). Therefore, they were also considered in the present study. Specifically, we assessed the following hypotheses: i) higher surface area will result in increasing diversity and abundance of associated epifaunal organisms; ii) higher structural complexity of gorgonians will result in increasing diversity and abundance of associated epifaunal organisms; iii) "colonial" epibiont cover (e.g. bryozoans, hydrozoans, sponges and macroalgae) of gorgonians has a relevant role in structuring attendant epifaunal assemblages; and iv) different taxonomic and or functional groups will respond differently to gorgonian attributes as they have different habitat requisites.

4.2. Materials and Methods

4.2.1. Gorgonian species selected and their attributes

The genera *Leptogorgia* and *Eunicella* have a worldwide distribution. For the purposes of the present study, the species *Leptogorgia lusitanica* and *Eunicella gazella* were selected, which are widely distributed in the region and among the most abundant gorgonians in the southern Portuguese coast (Cúrdia et al., sub.a). Although both species belong to the family Gorgoniidae, morphologically they are different: *Leptogorgia lusitanica* colonies are generally larger in width than in height, while *Eunicella gazella* colonies are more evenly shaped (i.e. display similar width and height). *Leptogorgia lusitanica* colonies may reach up to 80 cm in width, while *Eunicella gazella* is a small-sized species reaching a maximum of 35 cm in height. Branches of *Leptogorgia lusitanica* may have different colours, while *Eunicella gazella* branches are generally white and thicker.

In order to assess the effect of surface available for colonization we measured the height and maximum width of each colony and estimated the total surface area. Both, maximum height and width were measured in the laboratory, where each colony was photographed with a digital

camera at right angles (90°) using a tripod to keep a fixed linear distance to the gorgonian, maintaining scale. The estimation of the total surface area was based on the photos using the ImageJ software (Rasband, 2010). The estimation of the total surface area instead of volume resulted from the relative bi-dimensional structure of the gorgonians. Structural complexity was inferred by measuring fractal dimension (D), while lacunarity was calculated as a proxy for heterogeneity, based on the photos of each colony and using the ImageJ software. Specifically, for fractal analysis it was used the Box-Couting method, which involves laying a square mesh grid of various sizes (r), over the gorgonian image (fractal) to count how many boxes (N), are needed to cover it completely. To implement the Box-Counting Method, the plugin FracLac for Image J (Karperien, 2012) was used. The sizes of the square box forming the grid varied from 2 to 200 pixels using the following custom sizes (2, 4, 8, 10, 20, 50, 100 and 200). The number of boxes (N) that contain any part of the fractal object (gorgonian) were automatically counted for each iteration with different box sizes. The fractal dimension, which is characteristic of the morphology, i.e., the overall structure of the gorgonian colony, is defined as the structural fractal dimension (D)

$$D = \frac{\log N}{\log r}$$

and it was calculated by the program as the mean fractal dimension over 50 scans of differing grid positions. This fractal dimension is meaningful for objects with complex outlines such as gorgonians (Martin-Garin et al., 2007).

Lacunarity describes the texture of a fractal, using the size distribution of holes of that fractal. If a fractal has large gaps or holes, it has high lacunarity (Karperien, 2012). Lacunarity was calculated as:

$$E\lambda_r = 1 + \frac{{\sigma_r}^2}{\mu_r}$$

where σ is the standard deviation of the number of pixels and μ is the average number of pixels in squares of size r. During the calculation of $E\lambda$ the pixels of the image background were considered together with the object pixels. The mean lacunarity value was calculated for 50 grids of different origin.

Besides these morphological attributes, the abundance of macroscopic algae, cnidarians, bryozoans, sponges and hydrozoans was scored by a semi-quantitative index ranging from 0 to 4 (0 – absent; 1 – rare; 2 – common; 3 – abundant; 4 – very abundant). Scoring was always carried out by the same observer in order to minimize bias. For simplicity, this relative index will be hereafter designated as CEC (as for "colonial" epibiont cover, where the term colonial is used loosely to represent modular organisms). CEC will be used to infer the enhancement of functional intricacy of the gorgonian colonies derived from the presence of sessile organisms which may provide additional ecological niches and/or a greater variety of food resources for the attendant invertebrate assemblages. For each colony, CEC will be the sum of the scores of each epibiont

observed.

4.2.2. Study areas and sampling design

Sampling was undertaken in two consecutive summers (2010 and 2011), at Pedra da Greta (PG), the main rocky subtidal area in the central part of the Algarve coast, with approximately 3.6 km in length and ranging from 20–90 m in width and located at approximately 15 m depth (see Cúrdia et al., sub.a; Carvalho et al., sub., for more details). The summer period was chosen because it generally corresponds to the peak of invertebrates' diversity and abundance in this region. In each sampling period, 18 colonies of each species were collected with different length-sizes totalling 72 colonies. Each colony was enclosed in a plastic bag to prevent faunal loss and then carefully detached from the substrate. All gorgonians were transported to the laboratory for processing.

4.2.3. Biodiversity of attendant assemblages

In the laboratory the colonies were preserved in 96 % ethanol. All samples were washed through a 100 µm mesh sieve and colonies were observed under a magnifying glass to ensure that all fauna (mobile epifauna and colonial epibionts) and flora had been removed. All specimens associated with each colony were preserved in 96 % ethanol and afterwards identified to the lowest practice taxonomic level. To estimate species richness (i.e. the number of species per colony), unidentifiable organisms were, whenever possible, differentiated into different operational taxonomic units (OTUs). If animals were juveniles and/or were extremely damaged and it was not possible to recognize whether they were different entities or belong to any of the already identified species, they were not used in the analyses. The number of taxa and individuals per colony, as well as the (Hurlbert, 1971) expected number of species $ES_{(100)}$ were calculated both for the whole assemblage and for the main taxonomic groups separately (Arthropoda, Mollusca, Polychaeta). Feeding habits were also ascribed for all OTUs with more than 10 individuals, based on literature available.

4.2.4. Data analysis

In order to assess the relationship between gorgonian attributes (Table 4.1) and the biodiversity and abundance of the attendant epifaunal assemblage, Spearman rank correlations were performed. The best combination of gorgonian attributes explaining the diversity and abundance patterns of the attendant epifaunal assemblages were determined using a backwards-stepwise multiple generalized linear regression. This approach, recommended whenever co-linearity between independent variables is suspected (Haedrich et al., 2008), begins with a full model,

including all independent variables. Then, based on standard criteria, the variables failing at contributing to the explanation of the dependent variable (number of species or abundance) are systematically eliminated (Younger, 1979). The relationship between epifaunal feeding habits and CEC were analysed through regression analyses.

Table 4.1.: Minimum (min.) and maximum (max.) values for the gorgonian attributes considered in the analyses. *D*, fractal dimension; L, lacunarity; CEC, "colonial" epibiont cover. See text for further details.

Attributes	*Eunicella gazella*		*Leptogorgia lusitanica*	
	min.	**max.**	**min.**	**max.**
Area (mm^2)	507.28	12 851.13	496.85	24 316.12
Width (mm)	29.91	236.35	70.03	441.00
Height (mm)	53.51	223.64	51.27	445.00
D	1.52	1.81	1.58	1.79
L	0.93	2.99	0.81	4.84
CEC	0	28	0	30

4.3. Results

Attendant epifaunal assemblages were numerically dominated by arthropods, accounting for 48 % and 65 % of total abundance in *Eunicella gazella* and *Leptogorgia lusitanica*, respectively (Figure 4.1, top).

Molluscs were also abundant in both gorgonians (18 % in *Eunicella gazella* and 22 % in *Leptogorgia lusitanica*). On the other hand, the Platyhelminthes, which were exclusive of *Eunicella gazella* epifaunal assemblages, were the second most abundant group. In terms of species richness (i.e. the number of different OTUs), polychaetes were highly diverse, accounting for more than 30 % of total number of species on both gorgonians) (Figure 4.1, center). Indeed, in *Eunicella gazella* assemblages, polychaetes were the richest group (34 %), followed by arthropods (31 %) and molluscs (29 %). In *Leptogorgia lusitanica* colonies, arthropods were dominant, not only in abundance but also in number of species (35 % of total number of species), followed by annelids (33 %) and molluscs (27 %) (Figure 4.1, center).

Regarding the feeding guilds of the attendant epifaunal assemblages, in *Eunicella gazella* carnivores/omnivores and suspension-feeders/deposit-feeders were the dominant feeding modes (Figure 4.1, bottom). Epifaunal assemblages associated with *Leptogorgia lusitanica* colonies presented a more evenly distribution of the main feeding guild, that is to say that, besides the above mentioned trophic guilds, the contribution of deposit-feeders, deposit-feeders/herbivores and suspension-feeders was also relevant.

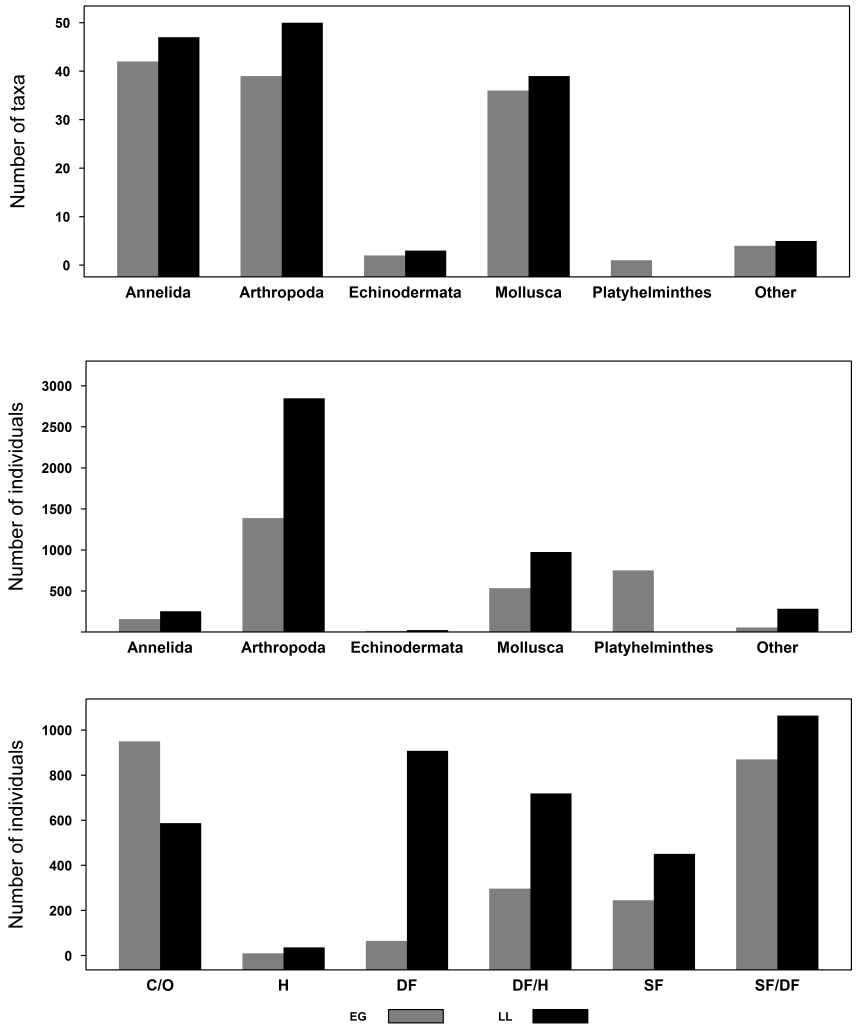

Figure 4.1.: Number of taxa (top), individuals (centre) and feeding guilds (bottom) of the dominant phyla observed in both gorgonian species. Others comprise data from Chordata, Cnidaria, Nematoda, Phoronida, Porifera and Sipuncula. EG – *Eunicella gazella*; LL – *Leptogorgia lusitanica*.

Hurlbert's expected number of species, which can be rarefied to the same number of individuals (equal or lower than the maximal common number of individuals), thus allowing comparisons of the assemblages sampled from colonies with different sizes, different surfaces available for colonization or different gorgonian species. Most of the rarefaction curves showed relatively steep slopes and are far from reaching the asymptotic values (species saturation) (Figure 4.2). By comparing the patterns of the rarefaction curves constructed for the three main taxonomic groups, it is apparent an increasing contribution of Polychaeta for biodiversity in both gorgonians, in comparison to the higher abundance of arthropods (Figure 4.2).

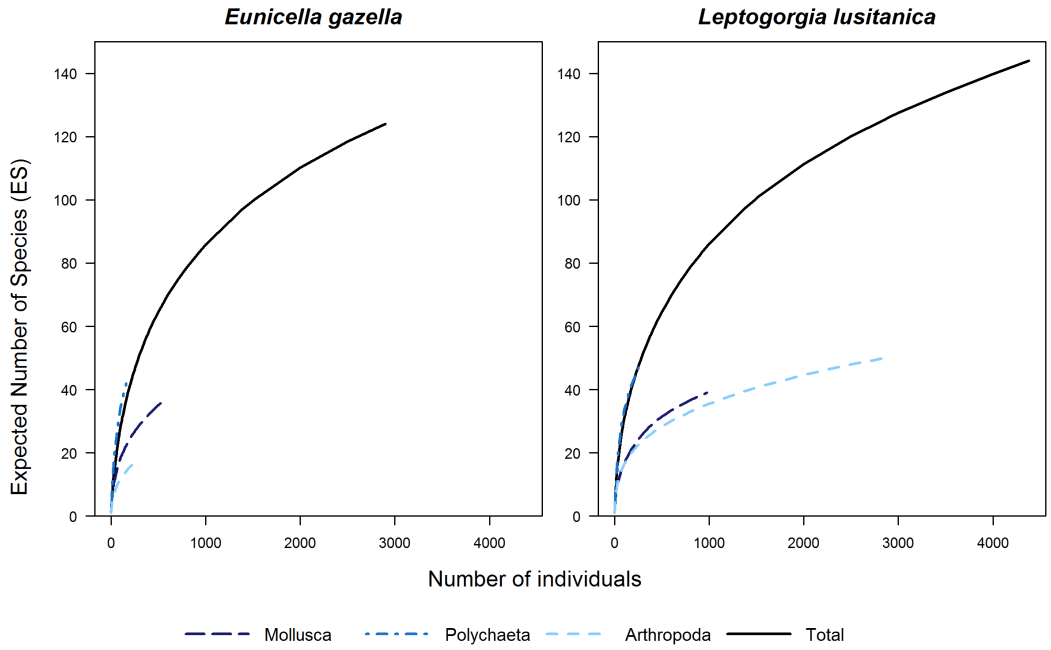

Figure 4.2.: Comparison of rarefaction curves (Hurlbert's expected number of species) for the all assemblage (Total) and the main taxonomic groups (Arthropoda, Mollusca and Polychaeta) in *Eunicella gazella* and *Leptogorgia lusitanica*.

Correlations between gorgonian attributes and the number of taxa and abundance were performed for the whole epifaunal assemblage and the main taxonomic groups separately. The correlation values were consistently highly significant for the relationships between both abundance and species richness of the attendant assemblages and functional intricacy (CEC index) in the two gorgonian species. The correlation between species richness and indicators of colonizable surface also showed significant values in most cases, with the highest values for height in *Leptogorgia lusitanica* and for area in *Eunicella gazella*. Abundance showed consistently lower correlation to the indicators of colonizable area and most values were not significant in *Leptogorgia lusitanica* (Tables 4.2 and 4.3). Except for the relationship between species richness and lacunarity in *Leptogorgia lusitanica*, measures of complexity showed no significant correlations to the attendant assemblages (Tables 4.2 and 4.3).

The radar plots (Figures 4.3 and 4.4) show absolute values of the maximum Spearman correlation within each category plotted on the three axes and the points are connected to present an area. These graphs illustrate the predominance of epibiont cover in explaining richness and abundance of epifaunal assemblages as well as the consistently higher correlations of gorgonian attributes with species richness than with abundance (Figures 4.3 and 4.4).

Table 4.2.: *Eunicella gazella.* Relationships between gorgonian attributes and species richness (number of taxa per colony) and abundance (number of individuals per colony) for all taxa and the main taxonomic groups separately. *D*, fractal dimension; *L*, lacunarity; CEC, "colonial" epibiont cover. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, ns – not significant.

	Area	**Width**	**Height**	***D***	***L***	**CEC**
Number of taxa						
All assemblage	**0.51****	**0.47****	**0.40***	0.26ns	-0.15ns	**0.79*****
Polychaeta	**0.43****	**0.37***	0.31ns	0.12ns	-0.05ns	**0.67*****
Arthropoda	**0.55*****	**0.47****	**0.44****	0.26ns	-0.12ns	**0.77*****
Mollusca	**0.39***	**0.38***	0.28ns	0.32ns	-0.22ns	**0.64*****
Number of individuals						
All assemblage	**0.41***	**0.40***	0.32ns	0.28ns	-0.19ns	**0.75*****
Polychaeta	**0.47****	**0.38***	0.31ns	0.13ns	-0.05ns	**0.62*****
Arthropoda	0.18ns	0.15ns	0.16ns	0.17ns	-0.12ns	**0.59*****
Mollusca	**0.44****	**0.43****	0.28ns	0.29ns	-0.20ns	**0.65*****

Table 4.3.: *Leptogorgia lusitanica.* Relationships between gorgonian attributes and species richness (number of taxa per colony) and abundance (number of individuals per colony) for all taxa and the main taxonomic groups separately. *D*, fractal dimension; *L*, lacunarity; CEC, "colonial" epibiont cover. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, ns – not significant.

	Area	**Width**	**Height**	***D***	***L***	**CEC**
Number of taxa						
All assemblage	**0.47****	**0.45****	**0.56*****	-0.23ns	**0.47****	**0.76*****
Polychaeta	0.29ns	0.27ns	**0.37***	-0.11ns	**0.37***	**0.69*****
Arthropoda	**0.51****	**0.52****	**0.62*****	-0.31ns	**0.43****	**0.65*****
Mollusca	**0.48****	**0.37***	**0.50***	-0.15ns	**0.38***	**0.63*****
Number of individuals						
All assemblage	**0.35***	0.32ns	**0.40***	-0.12ns	0.27ns	**0.77*****
Polychaeta	0.25ns	0.23ns	0.32ns	-0.06ns	0.31ns	**0.69*****
Arthropoda	**0.34***	**0.34***	**0.36***	-0.11ns	0.21ns	**0.50****
Mollusca	0.28ns	0.23ns	0.32ns	-0.04ns	0.19ns	**0.55*****

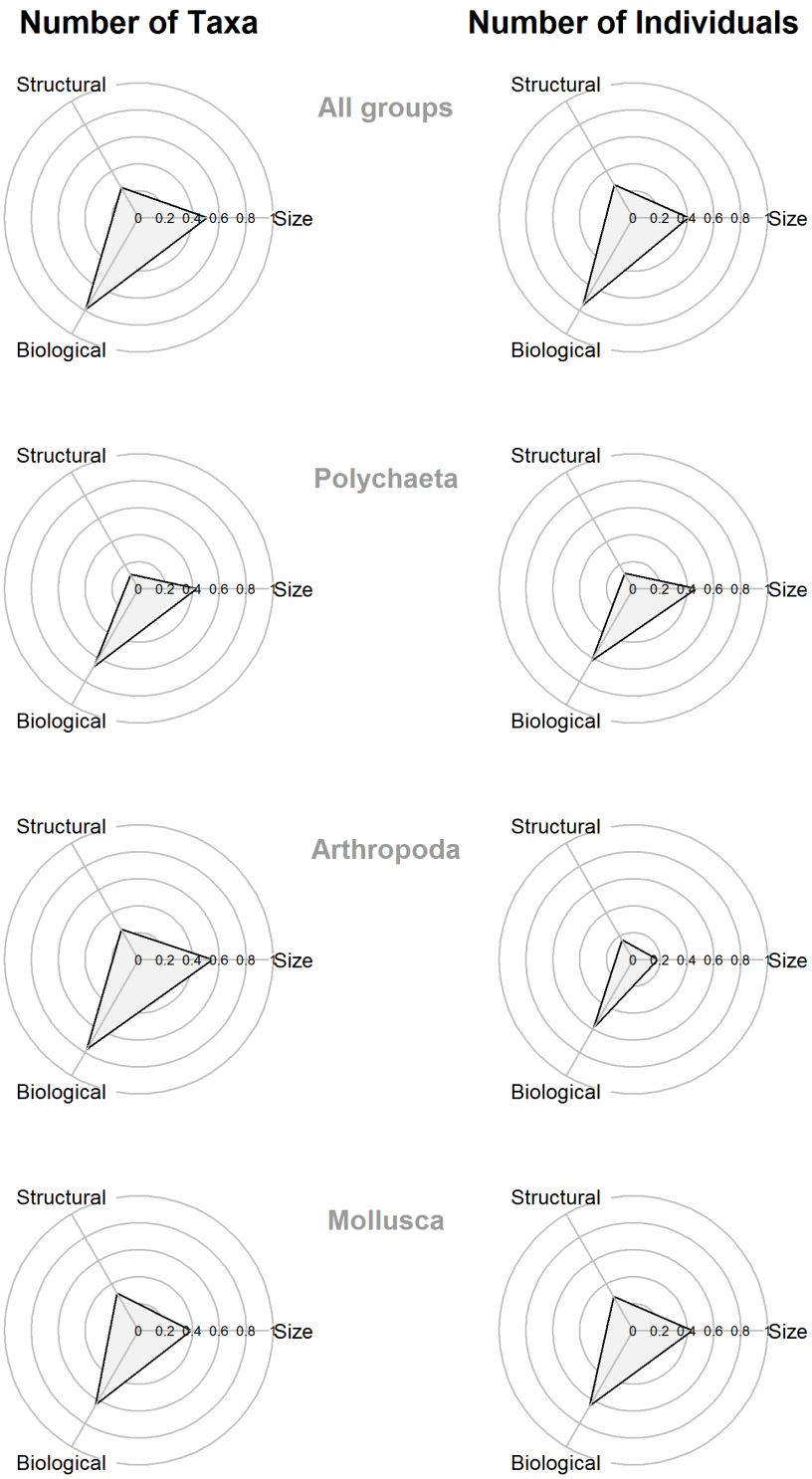

Figure 4.3.: *Eunicella gazella.* Radar plots of absolute maximum Spearman correlation within categories of size (total surface area, height, width), biological ("colonial" epibiont cover) and structural (fractal dimension, lacunarity) attributes. Data from Table 4.2.

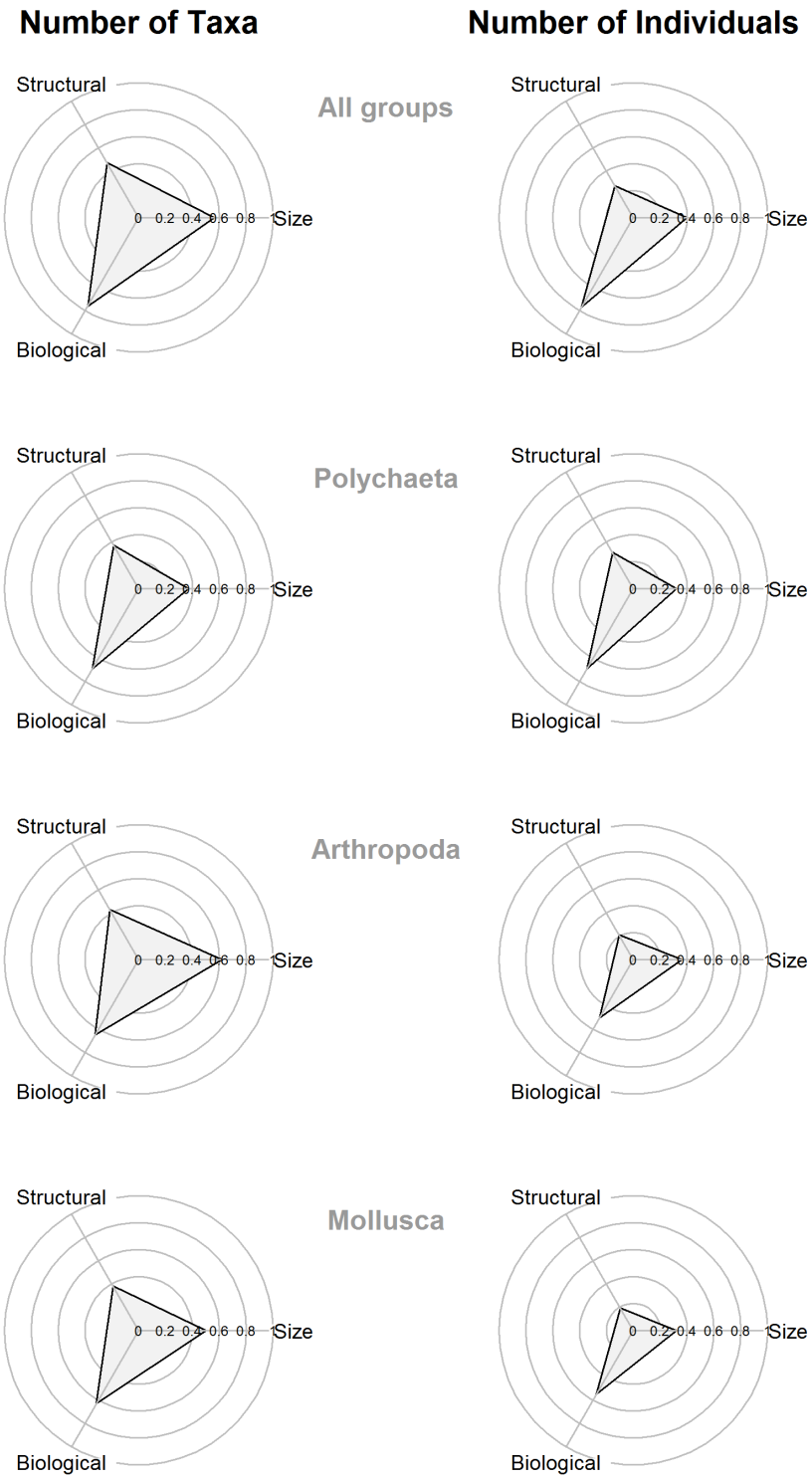

Figure 4.4.: *Leptogorgia lusitanica.* Radar plots of absolute maximum Spearman correlation within categories of size (total surface area, height, width), biological ("colonial" epibiont cover) and structural (fractal dimension, lacunarity) attributes. Data from Table 4.3.

Table 4.4.: *Eunicella gazella*. Subset of host attributes that explain most variability in number of species and number of individuals' patterns (backwards stepwise regression). Models for all faunal assemblage and those for the main taxonomic groups have been derived separately. The variables comprising the best model are listed in order of decreasing significance (p-values in parentheses). (−) indicates a negative relationship for a variable in the model. *D*, fractal dimension; *L*, lacunarity; CEC, "colonial" epibiont cover. $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

	Adj. R^2	Variables
Number of taxa		
All assemblage	0.649***	CEC $_{(0.0323)}$, Area $_{(0.2035)}$
Polychaeta	0.453***	CEC $_{(0.000)}$, Area $_{(0.161)}$
Arthropoda	0.683***	CEC $_{(0.000)}$, Area $_{(0.004)}$, −Width $_{(0.047)}$
Mollusca	0.397***	CEC $_{(0.000)}$
Number of individuals		
All assemblage	0.555***	CEC $_{(0.000)}$
Polychaeta	0.473***	CEC $_{(0.000)}$, Area $_{(0.006)}$, −D $_{(0.1191)}$, −Heigth $_{(0.1277)}$, −Width $_{(0.1573)}$
Arthropoda	0.335***	CEC $_{(0.000)}$
Mollusca	0.422***	CEC $_{(0.000)}$, Area $_{(0.126)}$

These trends were incorporated into multiple linear regression models to analyse the relationships between the attendant assemblage variables and gorgonian attributes (Tables 4.4 and 4.5). Again, CEC was always the variable that contributed the most for the total variability (Tables 4.4 and 4.5). It is also noteworthy that more variables were generally kept in the final model concerning *Leptogorgia lusitanica* assemblages, compared with those of *Eunicella gazella* (Tables 4.4 and 4.5) for which the best fits were obtained for CEC alone or combinations of CEC and area. Also, the significant contribution of complexity measures (*D* and *L*) were only detected for *Leptogorgia lusitanica* assemblages. Significant relationships between the abundance of individuals of the main trophic groups and CEC was found in the epifaunal assemblages associated with both gorgonians, except for the deposit-feeders in *Leptogorgia lusitanica* (Figure 4.5).

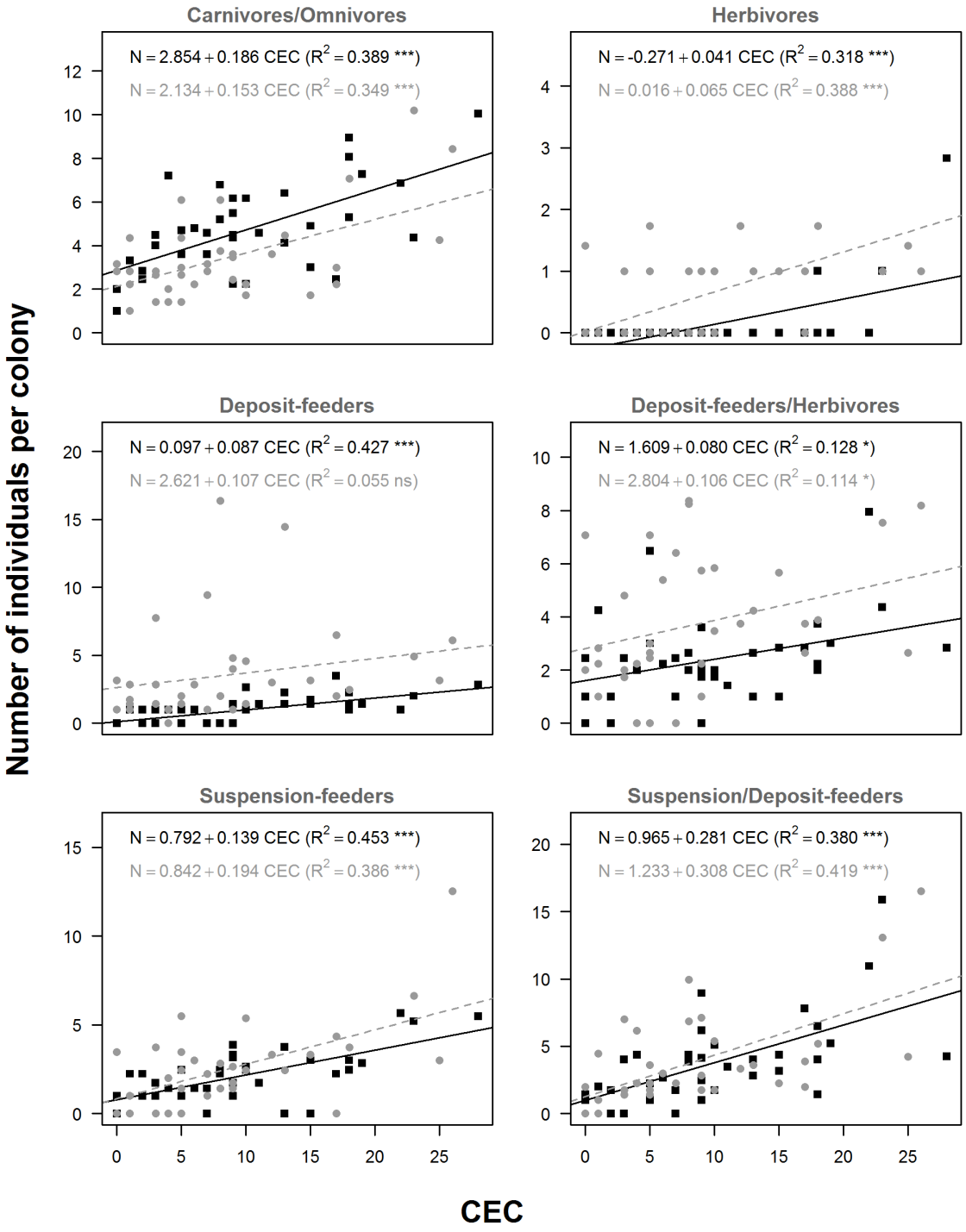

Figure 4.5.: Relationship between the abundance of individuals (square root-transformed) belonging to the main trophic groups and the "colonial" epibiont cover (CEC). The regressions are presented in black for *Eunicella gazella* (solid line) and grey for *Leptogorgia lusitanica* (dashed line). ns, not-significant; * $p < 0.05$, ** $p < 0.01$; *** $p < 0.001$.

Table 4.5.: *Leptogorgia lusitanica.* Subset of host attributes that explain most variability in number of species and number of individuals' patterns (backwards stepwise regression). Models for all faunal assemblage and those for the main taxonomic groups have been derived separately. The variables comprising the best model are listed in order of decreasing significance (p-values in parentheses). (−) indicates a negative relationship for a variable in the model. *D*, fractal dimension; *L*, lacunarity; CEC, "colonial" epibiont cover. $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

	Adj. R^2	Variables
Number of taxa		
All assemblage	0.652***	CEC $_{(0.000)}$, Area $_{(0.022)}$, −L $_{(0.0482)}$, −Width $_{(0.0549)}$, D $_{(0.1084)}$
Polychaeta	0.589***	CEC $_{(0.000)}$, L $_{(0.004)}$, D $_{(0.007)}$, Width $_{(0.0612)}$, Area $_{(0.1254)}$
Arthropoda	0.518***	CEC $_{(0.002)}$, Heigth $_{(0.004)}$
Mollusca	0.594***	CEC $_{(0.000)}$, Area $_{(0.001)}$, −Width $_{(0.003)}$, L $_{(0.042)}$, D $_{(0.1116)}$
Number of individuals		
All assemblage	0.333***	CEC $_{(0.000)}$
Polychaeta	0.531***	CEC $_{(0.000)}$, D $_{(0.011)}$, L $_{(0.030)}$
Arthropoda	0.228**	CEC $_{(0.002)}$
Mollusca	0.374***	CEC $_{(0.000)}$, Area $_{(0.056)}$, −Width $_{(0.062)}$

4.4. Discussion

The use of different measures of habitat complexity together with different sampling methods hampers direct comparisons of results gathered on the relationships between habitat complexity and associated animal assemblages. Besides, measures of structural complexity can change unpredictably across spatial scales and typical coral habitats are too complex for any single measure of complexity (Knudby and LeDrew, 2007). In coral reef systems, overall, species diversity of fish (Nagelkerken et al., 2000; Gratwicke and Speight, 2005a; Lingo and Szedlmayer, 2006; Wilson et al., 2007) and epifaunal invertebrate assemblages (Vytopil and Willis, 2001; Idjadi and Edmunds, 2006) have been positively correlated with habitat complexity. In some studies, results differed with the nature of the reef (Öhman and Rajasuriya, 1998) or were inconsistent in studied areas (Luckhurst and Luckhurst, 1978; Bejarano et al., 2011). Other studies also reported no relationship between species diversity and habitat complexity (Caballero and Schmitter-Soto, 2001). This inconsistency in the results obtained may be related to the use of different measures of complexity or the scales at which complexity was assessed, as, according to some authors (e.g. Knudby and LeDrew, 2007), it should preferably match the typical body size of the organisms whose habitat is being investigated. Although in the present study habitat complexity assessed by fractals was measured at the scale of the gorgonian colony, evidence of gorgonian habitat complexity leading to the enhancement of its attendant assemblage biodiversity was not unequivocal.

The present results demonstrate that gorgonian colony attributes affect species richness and

abundance of associated epifaunal assemblages in varying degrees. Moreover, this study also support the hypothesis predicting a differential response of different taxonomic groups to gorgonian attributes as a result of their different environmental and or biological requisites. The most striking pattern emerging from the results is that the colonial epibiont cover of gorgonians is always recovered as a significant and the most relevant attribute of the gorgonian habitat for the biodiversity and abundance of their attendant assemblages. Although multiple factors are expected to influence epifaunal assemblage patterns associated with gorgonians, the abundance of epibionts in each colony consistently enhanced diversity and abundance of all non-colonial species, although size measures (area, width and/or height) were also relevant. Despite some ascendancy of the structural complexity and heterogeneity measures in the multiple regression analyses (but only in *Leptogorgia lusitanica*), the biological structural component of the habitat was always the most relevant. This suggests that the enhancement of local diversity promoted by gorgonians may be also indirectly supported by these organisms that settle and grow up on the external surface of their skeletons. Associations of marine invertebrates and colonial animals, other than corals (Harvell, 1984; Lindberg and Stanton, 1988; Conradi et al., 2000; Dauby et al., 2001; Ribeiro et al., 2003), or even algae (Hall and Bell, 1988; Bologna and Heck Jr., 1999; Cacabelos et al., 2010) have been frequently reported, reinforcing the need for a better knowledge on the associations between corals and associated fauna. This possible dependency might reflect different faunal strategies to exploit the colonial epibiont organisms. Indeed, previous studies on the relationships between macroalgae/seagrasses and associated epifaunal assemblages reported that epiphytes (mainly algae) play an important role in structuring the patterns of distribution and abundance of mobile organisms (Schneider and Mann, 1991; Martin-Smith, 1993; Attrill et al., 2000; Cacabelos et al., 2010). These organisms can increase structural complexity (Hall and Bell, 1988; Schneider and Mann, 1991; Martin-Smith, 1993) and/or provide additional food resources (Kitting et al., 1984; Orth and Van Montfrans, 1984; Bologna and Heck Jr., 1999; Jones and Thornber, 2010), which will probably contribute to the maintenance of more diverse and abundant epifaunal assemblages. According to Rotjan and Lewis (2008), concerning scleractinian fauna, the 51 invertebrate corallivore species are in fact a small proportion of the total amount of invertebrate fauna described as being associated with coral species (Stella et al., 2011). For octocorals, namely gorgonians, it is also known that some gastropods feed on their hosts' living tissue (Patton, 1972; Burkepile and Hay, 2007; García-Matucheski and Muniain, 2010), but most of the other invertebrate-associated fauna does not (Patton, 1972; Kumagai, 2008). On the other hand, several amphipods, which were numerically dominant here, have been reported to feed on algae, bryozoans and hydrozoans (Duffy and Hay, 2000; Dauby et al., 2001). During a manipulative experiment testing the relative importance of trophic and structural characteristics of seagrass epiphytes on macrofaunal associated organisms, Bologna and Heck Jr. (1999) found that mobile seagrass fauna responded positively to the presence of new trophic resources, rather than the increases in secondary structure. Only caprellids (Crustacea: Amphipoda) appeared

to be associated with both the structure and trophic resources of epiphytes. Other authors, however, observed that both epiphyte cover and substratum shape were relevant in determining the distribution of epifaunal invertebrates in seagrass beds but responses were species-dependent (Schneider and Mann, 1991). In the present study, significant, yet sometimes weak, linear relationships were detected in both gorgonians between the abundance of the main trophic groups and the colonial epibiont cover. These results may indicate either their role as direct food resources or their contribution for the enhancement of additional food resources (e.g. animals for carnivores or organically rich particles for suspension/deposit-feeders) adding to the functional intricacy of the gorgonian habitat. Regardless the role of epibionts in structuring the epifaunal assemblages associated with gorgonians (i.e. food resource or additional habitat), the current results support the hypothesis predicting that gorgonians' epibiont cover (both flora and fauna) is relevant for the patterns of abundance and diversity of their attendant assemblages.

Despite the strong and consistent significance of epibiont cover, epifaunal abundance and diversity were also strongly related to gorgonian attributes representing the surface available for colonization, although not consistently between gorgonian species or across faunal groups. This relationship depended on the host considered as well as on the faunal group analysed. In the present study, regardless the measure used, the correlations between animal abundance and habitat attributes was always weaker than those found for diversity, which corroborates the findings of earlier studies (Öhman and Rajasuriya, 1998; Idjadi and Edmunds, 2006).

Taken into consideration the studies highlighting the relationship between structural complexity and diversity in marine environments both for fish and invertebrates, the non significant correlations between the fractal measure of complexity and both the number of species and abundance of invertebrate assemblages generally found could be surprising. Although this is the first attempt to apply fractal dimensions in estimating habitat complexity in coral colonies and to assess its relationship with associated epifaunal assemblages, this is a common approach to plants and algae (Morse et al., 1985; Gee and Warwick, 1994; Davenport et al., 1999; Attrill et al., 2000). Attrill et al. (2000) while assessing the relationship between seagrass structural complexity and the associated macroinvertebrate community found that seagrass biomass rather than complexity was the crucial factor for the enhancement of the number of individuals and species. As no significant positive relationship was detected between biomass and complexity, the authors linked the increase in species diversity with increasing seagrass biomass to a species-area relationship effect (larger surface area available for colonization). These authors proposed that the relationship between seagrass biomass and macroinvertebrate diversity was a sampling artefact resulting from the probability of collecting more of the rarer species as the area sampled increases. The results of the present quantitative, statistically-based study also suggest that the patterns of diversity and abundance of epifaunal assemblages seems to be better explained by a greater surface available for colonization and the enhancement of additional ecological niches (and food resources) promoted

by other colonial organisms and algae attached to the colonies than to the structural complexity of the colony itself. Nevertheless, if this may occur for gorgonian colonies, the paradigm that structural complexity enhances species diversity can still be valid if tested to a broader range of habitat complexity (e.g. by comparison to more complex coral species like scleractinians) or to a broader spatial scale (e.g. by comparison of the reef environment or gorgonian aggregation to other less complex habitats), as suggested for seagrass beds (Attrill et al., 2000). That is to say that this paradigm may be scale dependent. This is supported by some studies that analyzed coral reefs as a whole instead of focusing on the colonies themselves (Luckhurst and Luckhurst, 1978; Chabanet et al., 1997; Gratwicke and Speight, 2005b; Wilson et al., 2007). Besides, manipulative experiments on structural complexity using artificial reef blocks to create habitats with different levels of complexity also provided evidence supporting the hypothesis that habitat complexity increased the diversity of reef-fish species (Lingo and Szedlmayer, 2006). In the case of gorgonians, apparently their importance relies on the overall environment at the aggregation scale instead of the scale of individual colonies, which reinforces the need for the conservation of the gorgonian aggregation areas as a whole including their size structure and taxonomical diversity. Nevertheless, future research should attempt to compare corals of contrasting structural complexities (e.g. gorgonians versus scleractinian) and to separate the effects of habitat complexity, food availability and shelter in order to better assess the relationship between host attributes and associated epifaunal assemblages.

Acknowledgements

J.C. (SFRH/BD/29491/2006) and S.C. (SFRH/BPD/26986/2006) benefit from PhD and post-Doctoral grants, respectively, awarded by “Fundação para a Ciência e a Tecnologia” (FCT).

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Part III.

Reproductive aspects of gorgonians in the Algarve coast

CHAPTER 5

Reproductive cycle of the gorgonian *Eunicella gazella*: an originally tropical species dominating shallow Atlantic Iberian coasts

Abstract

The annual development of the reproductive structures of a shallow (16 m depth) population of the gorgonian *Eunicella gazella* was found to be highly synchronized between sexes. The sex ratio of 1.09 (F:M) was close to parity. The spermatogenic cycle took six to eight months but the oogenic cycle was much longer, taking more than one year for mature oocytes to develop. High fecundity was observed in females(27.30 ± 13.24 oocytes polyp^{-1}) and males (49.30 ± 31.14 sperm sacs polyp^{-1}) immediately before spawning, and these values are amongst the highest values to date in temperate gorgonians. Spawning occurred in September/October after a period of high sea surface temperatures. Females release high numbers of large sized mature oocytes (9.10 ± 4.60 oocytes polyp^{-1}) but retain immature oocytes that develop only in the next season. Fecundity was found to be correlated to polyp size but apparently not to colony size. Broadcast spawning is proposed as reproductive mode and no evidence of surface or internal brooding was observed. Even though common and abundant in the area, the colonies of *Eunicella gazella* frequently present high damage and the reproductive strategy of the species is discussed accordingly.

Keywords: gorgonians • *Eunicella* • reproduction • oogenesis • spermatogenesis • fecundity • spawning

5.1. Introduction

Demography and life-history traits shape the size of populations, having a huge impact on the persistence, decline, local extinction, and recovery of those populations. Reproduction is the main driver of most organisms, which invest large amounts of energy on progeny (e.g. Coma et al., 1998; Leuzinger et al., 2003; Harshman and Zera, 2007). The reproductive strategy is species dependent (or even population dependent), being shaped by biological, ecological and environmental factors, playing a crucial role in the population dynamics and biogeography of marine organisms (Grosberg and Levitan, 1992; Strathmann et al., 2002). Changes in patterns of recruitment may also have a major influence on the size of local populations (Hughes et al., 2000; Marshall and Keough, 2006), either increasing or decreasing them, and depending on the ecological role of the species, the effects can scale up to the community level (Grosberg and Levitan, 1992; Teixidó et al., 2011). In a marine species, the local degree of recruitment success depends on the stochastic variation of several environmental and biological factors, such as direction, frequency and speed of currents, availability of space, density of predators and phytoplankton biomass. However, the pool of recruits is governed primarily by the number of eggs

that can be fertilized, ultimately depending on the reproductive strategy of each species and local constraints (Lasker and Stewart, 1992; Levitan, 1993). Therefore, aiming at maximizing offspring, the reproductive cycle of a species integrates not only its evolutionary path (life-history) but also local constraints, in response to selective pressure.

The Anthozoa (Cnidaria) are one of the most conspicuous faunal groups in the marine environment, comprising approximately 7500 species (Daly et al., 2007). Gorgonians (Anthozoa: Alcyonacea) are important habitat builders as they provide structure, thus increasing the complexity of the system (Jones et al., 1994, 1997). They play an important ecological role in sublittoral benthic communities, providing habitat for other fauna and increasing the diversity and biomass of the community (Wendt et al., 1985; Cerrano et al., 2009). Their structuring role in temperate marine shallow ecosystems is linked to their population dynamics (e.g. density and size distribution), which are strongly influenced by reproductive aspects. The reproduction of cnidarians is diverse and can be very complex because of the high plasticity proportioned by their simple morphology and the lack of constraints common in higher metazoan taxa (Fautin, 2002). Even though octocorals may have the possibility to propagate asexually (a reproductive mode that may be highly underestimated, according to Fautin 2002), sexuality seems to be the norm in this subclass with approximately 3000 species (Daly et al., 2007), being highly retained during the evolutionary process (Kahng et al., 2011), similarly to what happens in scleractinian corals (Kerr et al., 2011). Gonochorism predominates in Octocorallia and hermaphroditism is rare, in marked contrast with hard corals (Scleractinia) where hermaphroditism is the most common type (for a review see Kahng et al., 2011). In octocorals, the reproductive mode (mating) is plastic, with nearly half of the species favouring broadcast spawning and the remaining being brooders (40 % internal and 11 % external) (Kahng et al., 2011). External brooding is thought to be an intermediate strategy between broadcast spawning (the original state) and internal brooding (Kahng et al., 2011), a strategy associated to more local dispersal (Szmant, 1986).

In species favouring sexual reproduction, gametes are necessary to ensure offspring to maintain populations but also to provide the genetic recombination to cope with environmental change (e.g. Coffroth and Lasker, 1998; Fautin, 2002). Therefore, gametogenesis and the traits associated to this process play a major role in reproduction. Because gorgonians are modular organisms and the polyp is finite in size, several traits such as the reproductive mode, number of reproductive structures and size govern the energy investment to enhance larval survival (Hall and Hughes, 1996; Leuzinger et al., 2003; Henry and Hart, 2005). For example, in octocorals, oocytes are generally large but oocyte size is not clearly related to sexuality, reproductive mode or polyp fecundity (Kahng et al., 2011). However, clades within octocorals present significant differences in oocyte size, suggesting that this trait is conserved along the evolution of these taxa (Kahng et al., 2011). On the other hand, polyp fecundity (number of oocytes or sperm sacs) may present significant differences at regional and local scales, reflecting differences in environmental factors

such as temperature (e.g. Gori et al., 2007, ress; Torrents and Garrabou, 2011). Therefore, energy allocation to reproduction is a complex task governed by internal and external factors and the interactions between them (Marshall and Keough, 2006). Identifying the main traits and drivers associated to the reproduction of a species is crucial for building specific models that can be used to predict the reproductive output of a determined species in a specific area.

Marine ecosystems face several pressures worldwide, such as overfishing, coastal development, pollution, tourism and climate change (e.g. Turner et al., 1999; Milazzo et al., 2002; Fox et al., 2003; Watling and Auster, 2005; Halpern et al., 2008; Mora, 2008), with differential response from the biota and complex networks of interactions between living resources and their habitats. There is evidence that gorgonian populations are affected by natural or/and anthropogenic factors (e.g. Coma et al., 2004; Linares et al., 2008a). Recently, it has been proven that shallow circalitoral areas in southern Portugal are characterized by a mixed population of gorgonian species (Gonçalves et al., 2010; Cúrdia et al., 2sub) and their conservation must be prioritized (Anonymous, 2011).

Natural and human disturbances are normally measured in terms of their effects on adult abundances and mortality rates, while the impacts on the reproductive biology and regenerative processes are usually ignored because they are less obvious (e.g. Hughes et al., 2000; Teixidó et al., 2011). Damage resulting from disturbance normally implies tissue regeneration that is energetically demanding (Linares et al., 2008a), and the allocation of energy for regeneration may impair not only the growth of the colonies but also their reproductive output, especially in larger colonies that sometimes are responsible for most of the reproductive output of a population (e.g. Hall and Hughes, 1996; Kapela and Lasker, 1999). It has been proven that disturbance decreases the reproductive output of these colonial organisms (e.g. Linares et al., 2005, 2008a; Torrents and Garrabou, 2011; Tsounis et al., 2012) with serious effects in their population dynamics and conservation (Tsounis et al., 2006; Linares et al., 2008b). Localized changes that affect coral reproduction at one location may also have important effects on nearby populations because of the strong link between benthic and larval stages (Hughes et al., 2000). In fact, small changes in coral fecundity can result in large changes in recruitment leading to dramatic effects of large magnitude (Hughes et al., 2000).

Management of coastal areas where ecosystem engineers are present should always take into account the dynamics of those species, and the processes affecting the stocks of adults, namely recruitment. Because of the importance of gorgonian species for the Mediterranean coralligenous reefs (Bavestrello et al., 1997; Linares et al., 2005, 2007; Ballesteros, 2006), several reproductive aspects of the most abundant gorgonian species have been addressed in the recent past (e.g. Coma et al., 2004; Tsounis et al., 2006; Ribes et al., 2007; Linares et al., 2008a) in order to provide baseline data and fulfil knowledge gaps. In contrast, such information is missing for common species from the Atlantic coast of the Iberian Peninsula, such as *Eunicella labiata*, *Eunicella*

gazella and *Leptogorgia lusitanica* (Cúrdia et al., 2sub). Because *Eunicella gazella* is one of the most affected gorgonian species in the south Portugal (unpublished data), presenting both high damage frequency (percentage of damaged colonies) and extension (percentage of the colony area damaged), knowledge on the reproductive processes of this species is crucial for understanding the life-history patterns of the species and a preliminary step towards assessing the ability of these species to recover from disturbances. In this context, the current study aims at describing the reproductive cycle of *Eunicella gazella*, a poorly studied species, namely concerning oogenesis, spermatogenesis, fecundity and time of spawning. The reproductive aspects analysed in this study will be discussed in terms of their importance for the distribution of the species in the context of areas under multiple pressures.

5.2. Materials and Methods

5.2.1. Study area

The collection of samples was undertaken in Pedra da Greta, a rocky area used as fishing ground located near Faro, southern Portugal. This rocky formation extends for nearly 3 km long, ranging from a few metres in width to 80 m in the widest areas, and a depth range of 14–18 m. Geologically, the elevated surface represents a fossilized ancient dunar belt that went underwater with sea-level rising long time ago, constituting one of the largest hard-bottom areas in the eastern part of the Algarve coast. The area is characterized by numerous small canyons running parallel and perpendicularly to the coast creating a "giants' causeway" bottom, with vertical relief varying from 0.3 to 4 m. Considerable topographic complexity is provided by such 3-dimensional arrangement, resulting in numerous small holes, caves and overhangs that provide refuge for a large number of species, including several commercially important species. Professional fishermen use a wide variety of fishing gears in this reef (e.g. trammel nets and gill nets, hook lines, pots and cages, jiggling) but recreational fishermen also use this area, especially during summer. This constant fishing activity results in large quantities of lost fishing gears in the bottom, but also in direct damage to gorgonian colonies. Damaged colonies are very frequent in this area, presenting extensive partial mortality, overgrowth and/or signs of breaking (many times loosing more than half of the colony).

5.2.2. Sampling

Samples were collected monthly from July 2009 to July 2010. Winter months (November to February) were characterized by frequent periods of bad weather that did not allow sampling in

two dates, November 2009 and February 2010. At each sampling period, fragments of the apical part of 30 colonies of *Eunicella gazella* were collected by SCUBA diving, selecting colonies that were not extensively damaged and without clear signs of faunal overgrowth. The maximum height (nearest cm) of each sampled colony was recorded. Biological material was preserved in 10 % buffered formalin until further analyses.

5.2.3. Reproductive cycle and fecundity

Although the term "gonads" has been widely used in scientific publications regarding anthozoans, according to Fautin and Mariscal (1991) the so-called gonads are simply gametogenic areas of the mesenteries. The equivalence of each individual oocyte (or spermary) to a single gonad in order to quantify fecundity and other reproductive parameters should be avoided in future contributions. The term "reproductive structures" is used in those cases where no special reference is made to one of the sexes.

The oogenic cycle was studied over a 13 month period, with 11 sampling periods (mentioned above). For the spermatogenic cycle, 6 time periods (July, September and October 2009; January, April and July 2010) were analysed. For both sexes, a total of 5 colonies was analysed at each sampling date. Spicules were de-calcified using a 10 % formic acid solution diluted with 4 % formalin. For each colony, 10 randomly chosen polyps, located at 1–5 cm of the branch tip were dissected under a stereo microscope. For each polyp, reproductive structures (oocytes or spermaries) were counted under the stereo microscope at full magnification (50×). The polyp content was then placed on a microscope slide with a drop of 10 % lactic acid and covered with a cover slip. The preparation was observed only 24 h after this procedure to allow the lactic acid to degrade the tissues, thus making easier the detection and identification of the oocytes or spermaries. The maximum and minimum diameters of all reproductive structures were measured with an eyepiece micrometer.

Oocytes and spermaries were spherical or ellipsoidal in shape, therefore the equivalent diameter of the ellipse (D) was estimated using the formula:

$$D = \frac{AB}{3(a+b) - \sqrt{(3a+b) \times (a+3b)}}$$

where A is the maximum diameter; B is the minimum diameter; a is $\frac{A}{2}$ and b is $\frac{B}{2}$.

The volume of each oocyte or spermary was estimated using the formula:

$$V = 0.75\pi \times (0.5D)^3$$

where V is the volume of oocyte or spermary and D is its equivalent diameter. Finally, the volume of oocytes or spermaries per polyp was calculated as the sum of the volume of the oocytes or spermaries.

Development of reproductive structures in both sexes was also analysed using histological techniques. Before processing tissue samples for histology, gorgonian spicules were de-calcified using a solution of 10% formic acid in 4% buffered formalin and the axis of the colonies was carefully removed with fine pointed tongs. Small pieces of tissue were dehydrated in a graded ethanol series and embedded in paraffin. Tissue sections of 10 µm thickness were cut in a microtome and left to dry in the oven at 37 °C for at least 48 h. Histological cuts were stained using the Hematoxylin and Eosin (HE) method (Kiernan, 1990).

In this study, fecundity is defined as the number of oocytes (or spermaries) in a polyp over a reproductive season, following the recommendations of Llodra (2002) to obtain the maximum information of the data analysed.

5.2.4. Environmental data

Monthly data on sea surface temperature (SST), chlorophyll *a*, photosynthetically available radiation (PAR) and particulate organic carbon (POC) during the study period were used for correlations with the gametogenic cycle. Data on SST was gathered from the oceanographic buoy located at ≈ 2 nautical miles from the study area (www.hidrografico.pt/boias-ondografo.php). Chlorophyll *a* concentrations, PAR and POC were derived from satellite remote sensing data, collected from the Giovanni online data system (MODIS-Aqua 4 km, monthly processed data, available at http://disc.sci.gsfc.nasa.gov/giovanni/overview/index.html), developed and maintained by the NASA Goddard Environmental Sciences Data and Information Services Center - GES DISC (Acker and Leptoukh, 2007). Chlorophyll *a* and POC data are used as proxies for primary production (phytoplankton) and secondary production (zooplankton).

5.2.5. Statistical analyses

The sex ratio was compared with parity (1F:1M) using the χ^2 test (Wilson and Hardy, 2002). The non parametric Kruskal-Wallis' U test was employed to compare colony size, the number of reproductive structures per polyp, volume of oocytes or spermaries and polyp equivalent diameter between sampling periods. Multivariate comparison tests were performed whenever significant differences were detected.

In some monthly sampling periods, the size-frequency distribution of oocyte diameters (equi-

valent diameter of ellipse) presented two modes. In order to separate the two components of the mixed distribution, the method described by Macdonald and Green (1988) was used. This method employs grouped data to find the best fit for component distributions to histogram data (in this case comparing a single mode against two modes), using chi-squared approximation to the likelihood ratio test. We used mixdist (Macdonald and Green, 1988), using grouped data (size classes of 20 µm) to calculate the parameter values (α, relative percentage; μ, mean; σ, standard deviation) and their standard errors for each component distribution. The program returns a chi-square value for the fit between calculated and empirical histograms. Log-normal distributions were used as they presented better fits and because in the absence of bi-modality, the distribution of data follows the log-normal model.

Regression analysis was used to assess the relationship between colony size, fecundity and volume of reproductive structures in both sexes. The effect of polyp size on fecundity and oocyte volume was also analysed using regression analysis at two different periods (May-June and July-August, with grouped data to increase statistical power). Analysis of covariance (ANCOVA) was employed to test the effect of colony size on these correlations (Bingham and Fry, 2010).

All analyses were performed in the open source statistical software R v2.14.1. (R Development Core Team, 2010), with statistical significance set for $p < 0.05$.

5.3. Results

5.3.1. General features and sex ratio

In general, all fertile polyps from a colony exhibited reproductive structures of the same sex (gonochoristic). However, one colony from June 2010 identified as female in the stereo microscope, presented both oocytes and small spermaries (hermaphroditic). Within this hermaphroditic colony, all individual polyps analysed (n=10) presented both sperm sacs and oocytes. This colony was not considered for estimating the number of reproductive structures per polyp, their volume and size frequency distribution. Although the sexes are separate, colonies lacked any obvious secondary sexual character and the reproductive structures are the only indications of gender. The sex ratio was 1.09 ($\chi^2 = 0.268$, $p = 0.604$), not deviating significantly from parity (1F:1M).

Medium and large-sized oocytes (≥150 µm) are visible under the stereo microscope (50× magnification) and tend to form small aggregates composed by a few different sized cells growing from the mesenteries. When observed under the microscope (Figure 5.1), these aggregates are dominated by small-sized cells that are mostly overlooked in the stereo microscope. Those small-sized cells correspond to pre-vitelogenic cells (80–160 µm diameter) and are characterized by clear

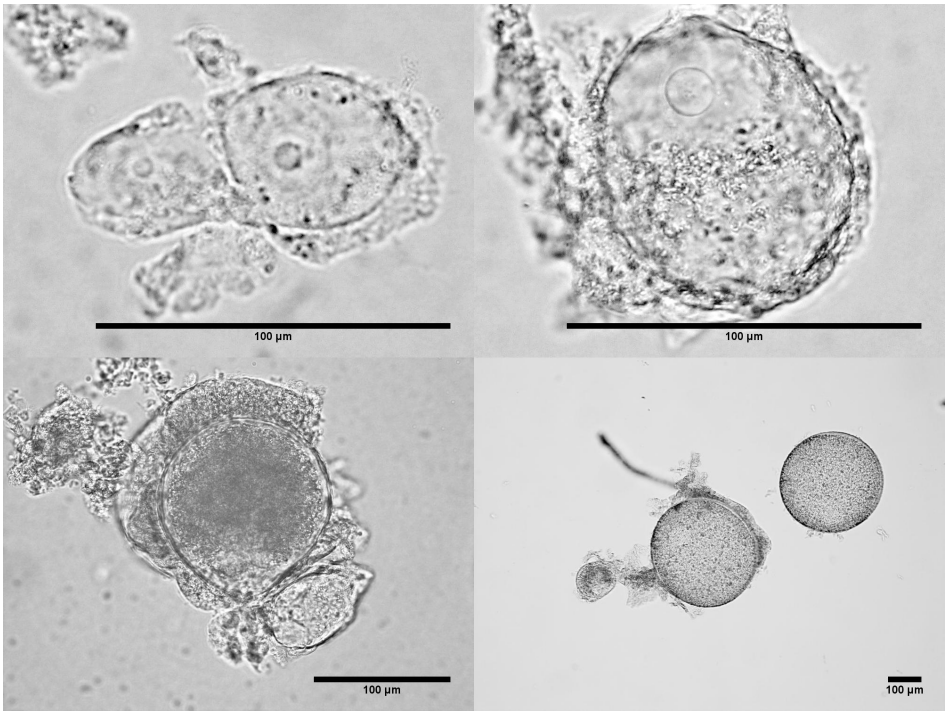

Figure 5.1.: Female reproductive structures of different size. The nucleus and nucleoles are visible in smaller oocytes. A drop of 10 % lactic acid was added to the preparation to clarify the tissues.

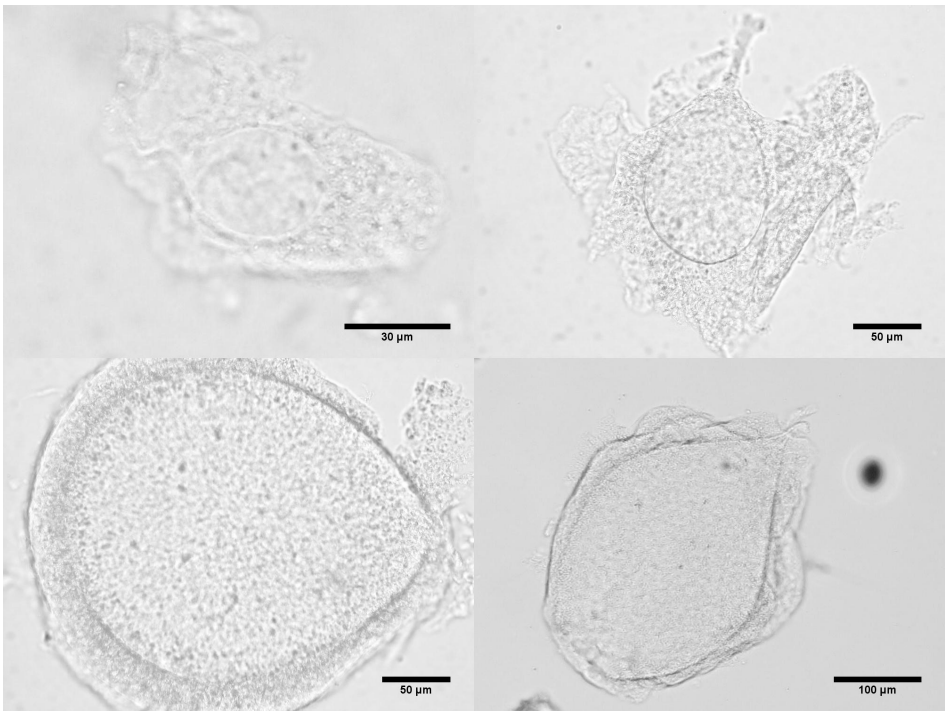

Figure 5.2.: Male reproductive structures (sperm sacs) of different size. Gastrodermis is more abundant around larger sperm sacs. A drop of 10 % lactic acid was added to the preparation to clarify the tissues.

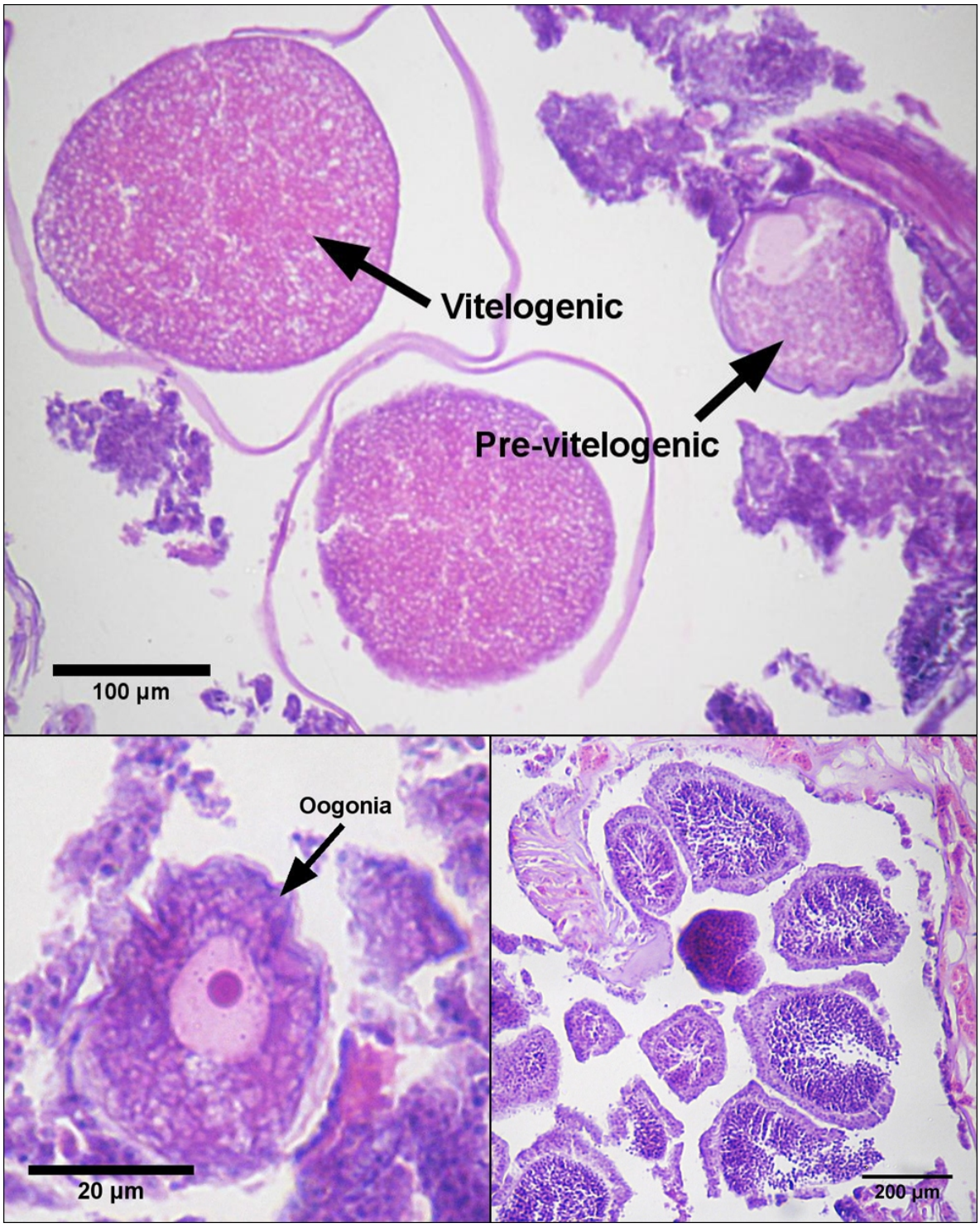

Figure 5.3.: Histological micro-photographs of female (top and bottom left) and male (bottom right) reproductive structures of *Eunicella gazella*. Oogonia, pre-vitelogenic and vitelogenic oocytes are presented. Sperm sacs of different size showing similar development, the lumen of the sperm sac is dominated by spermatocytes.

cytoplasm and a large nucleus with two evident nucleoli and are basophilic. Oocytes larger than 250 µm diameter presented a thick cytoplasmic membrane (5–10 µm), yellow opaque colour and were granulated in texture. Histologically, these eosinophilous cells correspond to vitelogenic and mature oocytes (Figure 5.3). The cytoplasmic membrane of some of the large oocytes was easily damaged during manipulation, resulting in abundant lipidic droplets in the disrupted area.

Concerning males, gastrodermis surrounding the reproductive structures over the mesentery clearly decreases during gametogenesis, being abundant and clearly identifiable in the first stages and almost absent in ripe spermaries (Figure 5.2). With experience, it was possible to distinguish the gastrodermis of male from that of female colonies, based on the morphology and development. Smaller sperm sacs (25–130 µm) are ellipsoid in shape and present a thin layer of tissue surrounding several large and slightly irregularly shaped spermatogonia. Sperm sacs with 140–300 µm present a thick layer of tissue (5–10 µm) surrounding large numbers of spermatocytes, which are identifiable in the microscope even without processing the material for histology. Larger sperm sacs normally do not present gastrodermis tissue in their surroundings (Figure 5.2), are opaque and with a darker colouration, but cells cannot be differentiated without processing the material for histology. Large sperm sacs in samples of August 2009 were dominated by spermatocytes, whereas sperm sacs of equivalent dimensions in samples of September and October 2009 presented mostly spermatozoa and a few spermatocytes. When fully developed, the larger sperm sacs are quite irregular in shape and very easily disrupted.

5.3.2. Annual cycle of oocyte development

Oocytes developed attached to the mesenteries by a short mesogleal stalk at the base of each polyp. Formation of new oocytes was not synchronous and took place over a six to seven month period (February-March until September-October) (Figures 5.4 and 5.6). The newly formed oocytes (80–160 µm diameter) remained at approximately the same size until January of the following year (Figure 5.6). Between March and May, the previous year's cohort of oocytes increased up to 300 µm in average diameter (Figure 5.6). From June to September these oocytes continued to mature, increasing their size and volume, and reaching maximum values in September (≈500 µm) (Figures 5.5 and 5.6 and Table 5.1). In October, these large oocytes were released and the size-frequency distribution is almost entirely composed by the new oocytes produced in the current season (Figure 5.6 and Table 5.1). This pattern was also evident in the mean volume of oocytes per polyp, which increased markedly from March to June and July to September (Figure 5.5).

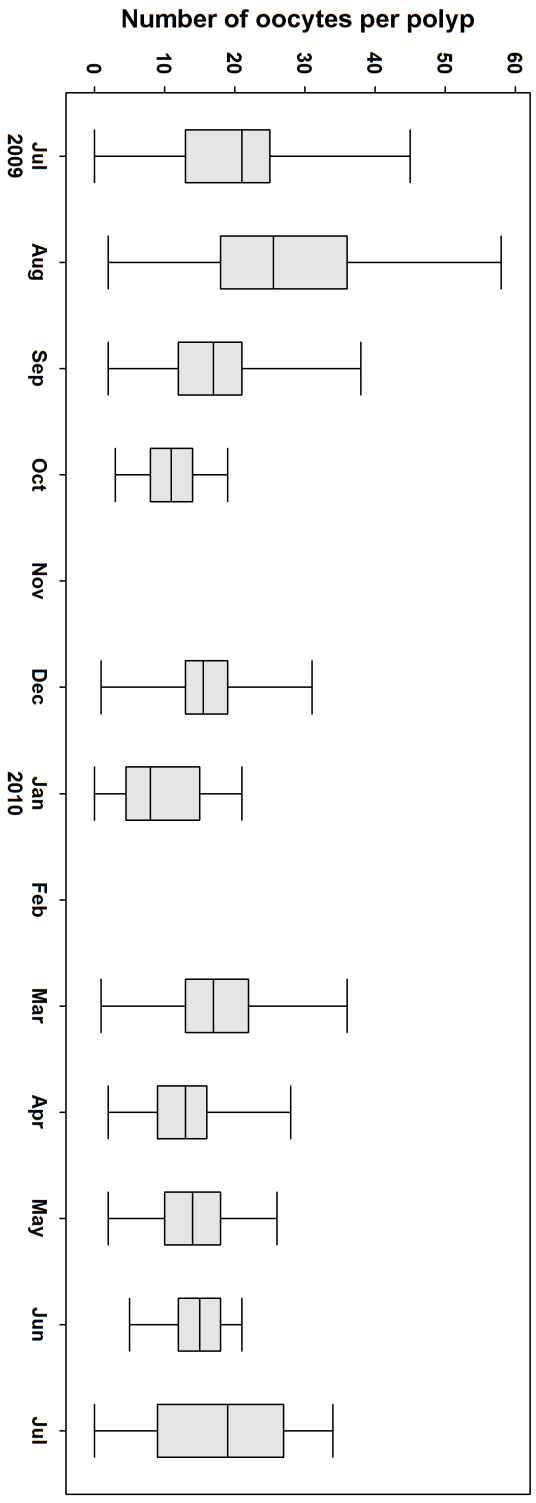

Figure 5.4.: Boxplots of the number of oocytes per polyp during the study period. The central line represents the median; the box represents the 50 % interquartile range of observations and the whiskers represent the minimum and the maximum values.

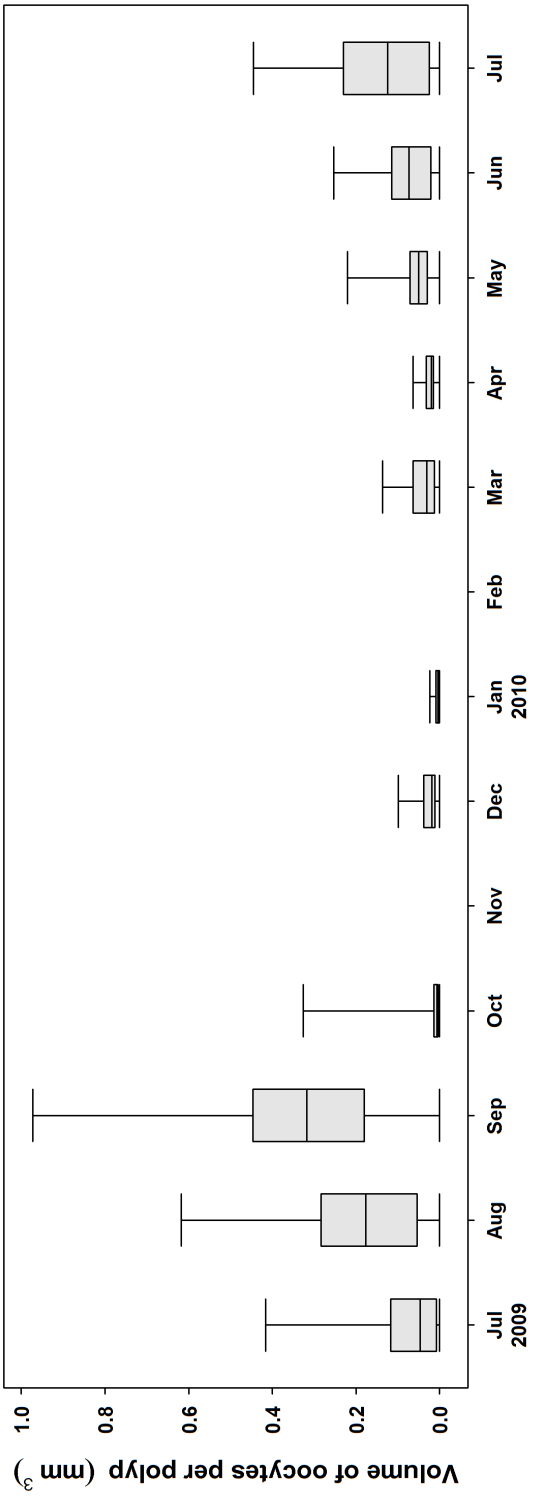

Figure 5.5.: Boxplots of the volume of oocytes (mm^3) per polyp during the study period. The central line represents the median; the box represents the 50 % interquartile range of observations and the whiskers represent the minimum and the maximum values.

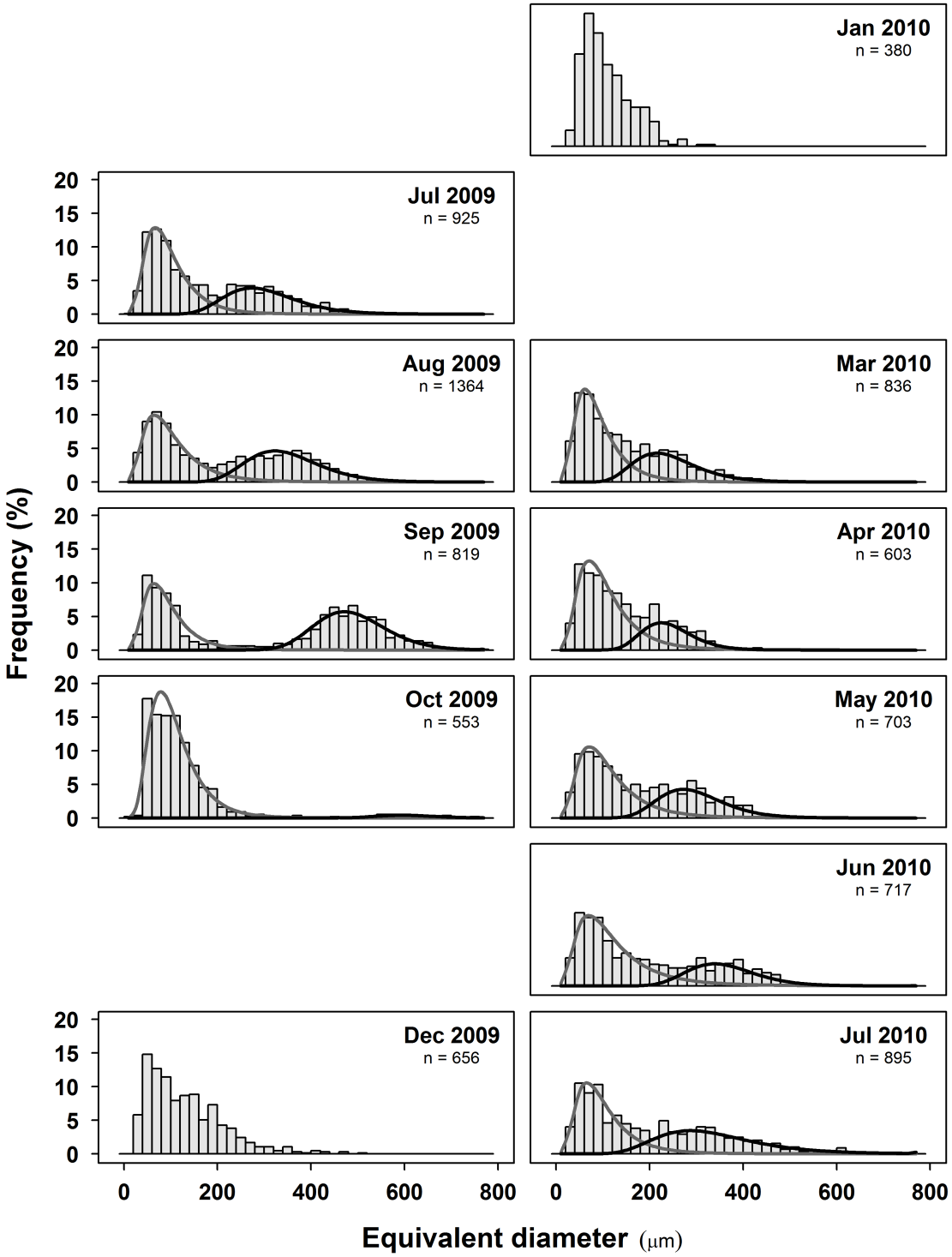

Figure 5.6.: Size-frequency distributions of the equivalent diameter of oocytes (μm) showing the mixture of two log-normal distributions fitted to histogram data (black line, cohort of the current reproductive season; grey line, cohort of immature oocytes).

Table 5.1.: Variation over time of the proportion (p_i), number (n), average size (μ), diameter in mm, and standard deviation (σ) of oocyte cohorts from ten polyps of each of five female colonies (50 polyps total) from the *Eunicella gazella* population. Cohorts were distinguished using finite mixture distribution models (see text for more details).

		Cohort 1				**Cohort 2**				**Cohort 3**				χ^2	p
		p_i	n	μ	σ	p_i	n	μ	σ	p_i	n	μ	σ		
July		0.370	342	304.4	82.89	0.630	583	98.0	53.21	-	-	-	-	30.95	0.569
August		0.451	616	350.3	82.65	0.549	748	105.6	65.62	-	-	-	-	43.66	0.102
September		0.539	442	489.6	77.62	0.461	377	93.6	50.73	-	-	-	-	69.51	**0.000**
October		0.031	17	605.6	62.09	0.969	536	108.4	53.40	-	-	-	-	66.20	**0.001**
December		-	-	-	-	1.000	656	132.3	92.40	-	-	-	-	-	-
January	2010	-	-	-	-	1.000	380	109.6	55.11	-	-	-	-	-	-
March		-	-	-	-	0.361	302	245.4	74.18	0.639	534	91.8	51.49	27.27	0.748
April		-	-	-	-	0.269	162	242.7	56.15	0.731	441	107.9	62.52	25.14	0.835
May		-	-	-	-	0.367	258	297.5	73.89	0.633	445	114.6	70.89	27.83	0.722
June		-	-	-	-	0.298	214	361.7	76.19	0.702	503	125.3	86.88	48.52	**0.040**
July		-	-	-	-	0.445	398	340.5	118.36	0.555	497	102.3	60.54	59.14	**0.003**

5.3.3. Annual cycle of spermaries development

In January, 90 % of the polyps presented reproductive structures, but the number of spermaries per polyp was very low and their volume was extremely reduced (Figures 5.7 and 5.8 and Table 5.2). From January to September, spermary number and volume increased sharply. In September, spermaries were ripe and very abundant (14–159, mean of 49.3 spermaries per polyp). In October, the number of spermaries declined sharply coincident with the end of spermatogenesis and gamete release, but volume was still high because of some large spermaries present in many polyps.

These results were confirmed by the size-frequency distribution of the sperm sacs diameter. In January, newly developed small-sized structures (20–120 µm in diameter) were predominant in the size-frequency distribution. The development of those spermaries was evident in April and July, as distributions showed progressively longer tails to the right and lower contribution of new structures (Figure 5.9). The production of new spermaries was halted between July and September (similar number of sperm sacs per polyp). In September, the size distribution of sperm sacs was mesokurtic, with slight negative skewness and a large range of diameters (20–624 µm), but a very low contribution of small-sized sperm sacs (20–120 µm representing less than 20 %). In October, the release of spermatozoa produced a negatively skewed distribution with a narrower range of sizes. Spermatogenesis took between eight and ten months to complete, and thus was much shorter than oogenesis.

5.3.4. Fecundity

From the oogenic cycle it was observed that mature oocytes (greater than 350 µm) were spawned by late September/October. The mean number of mature oocytes per polyp in September was 9.1 ± 4.60 (SD). Considering that the mean number of polyps in a terminal branch is 27.5 cm^{-1}, the estimated number of mature oocytes per cm of *Eunicella gazella* in the studied area is roughly 250. The size of mature spermaries is more difficult to estimate since, histologically, spermatozoa were observed in spermaries presenting a wide size range. However, considering the size-frequency distribution of spermaries in September and October, it is expectable that in September sperm sacs greater than 300 µm are mature, resulting in 18.8 ± 11.81 sperm sacs per polyp and ≈ 520 mature male reproductive structures per cm of *Eunicella gazella*, i.e. more than twice the number of mature oocytes. Nevertheless, male fecundity estimates are most likely underestimated as the limit of 300 µm is probably too conservative.

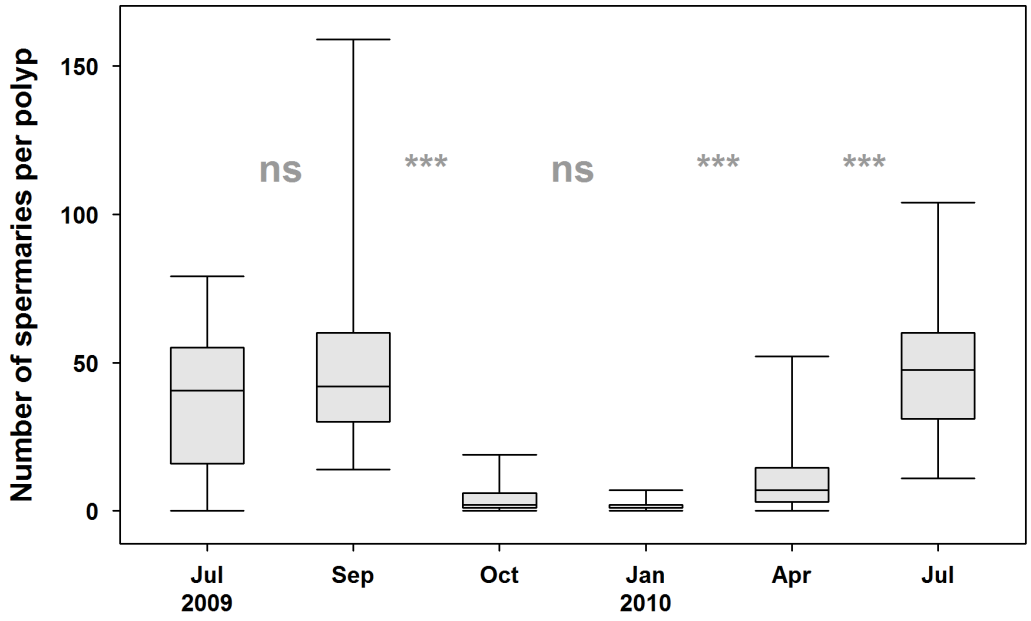

Figure 5.7.: Boxplots of the number of sperm sacs per polyp during the study period. The central line represents the median; the box represents the 50 % interquartile range of observations and the whiskers represent the minimum and the maximum values.

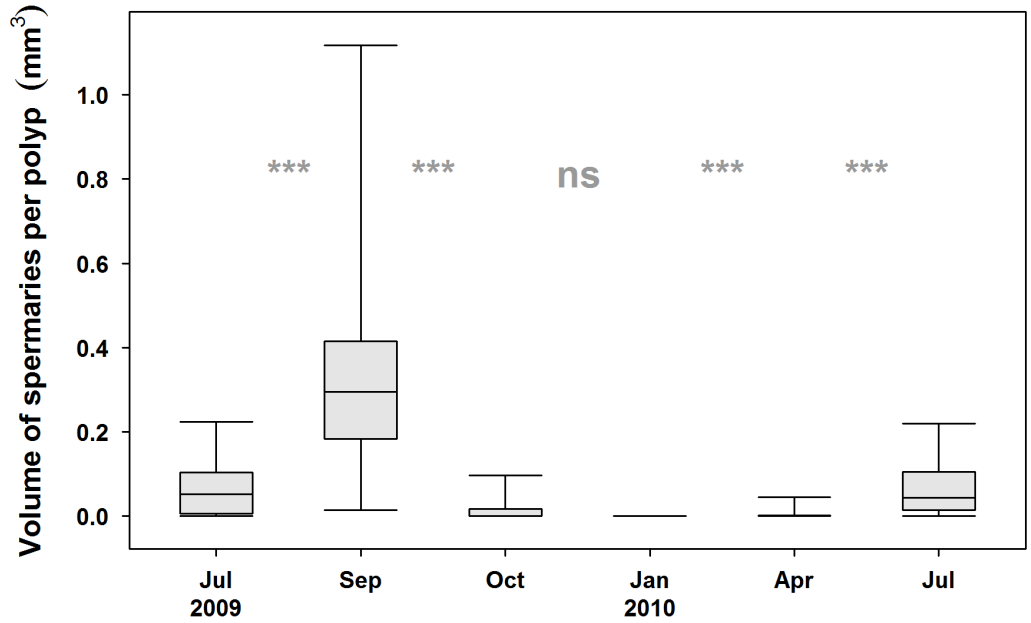

Figure 5.8.: Boxplots of the volume of sperm sacs (mm^3) per polyp during the study period. The central line represents the median; the box represents the 50 % interquartile range of observations and the whiskers represent the minimum and the maximum values.

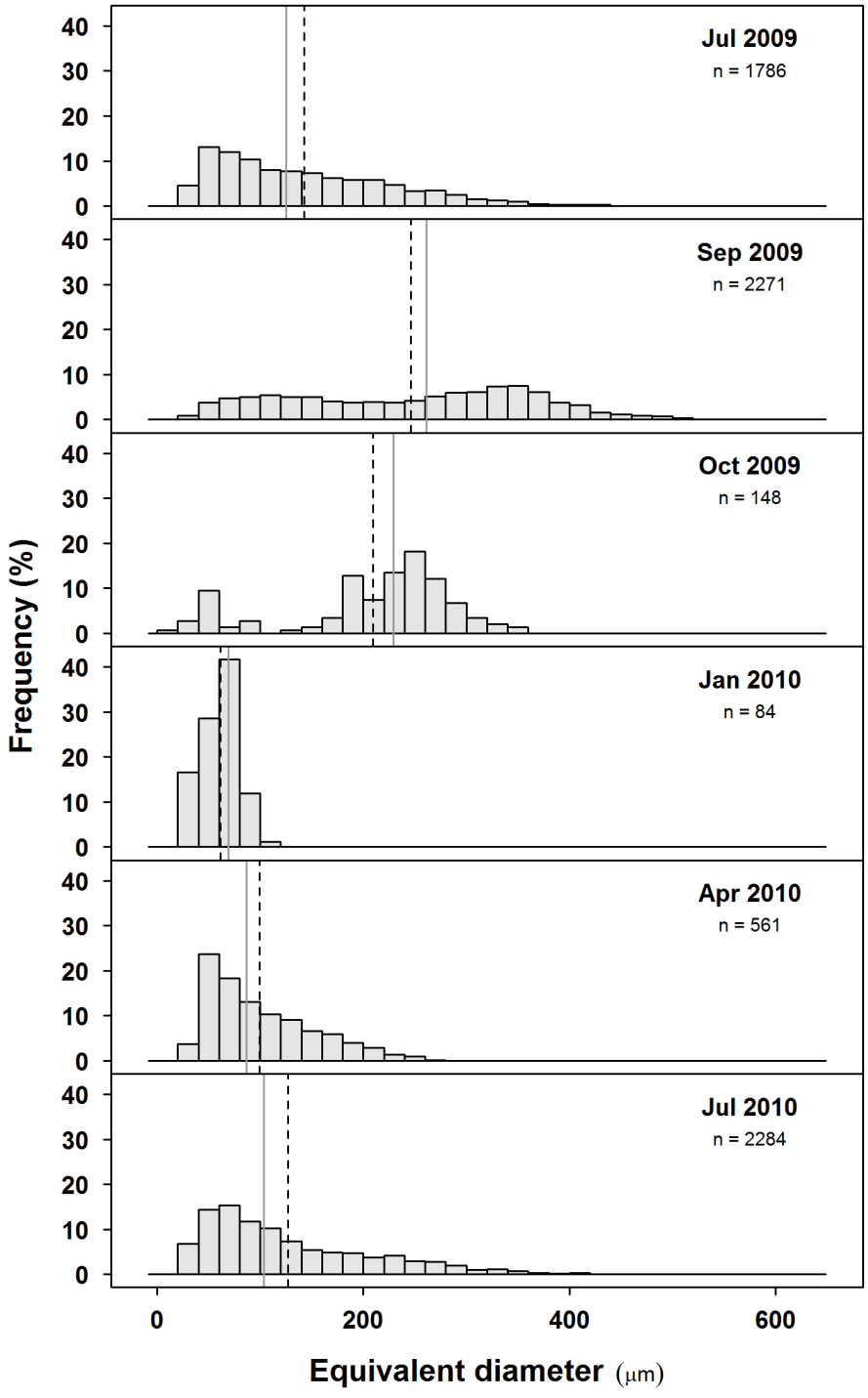

Figure 5.9.: Size-frequency distribution of the equivalent diameter (μm) of sperm sacs for each sampling period. The solid and the dashed lines represent the median and mean value, respectively.

Table 5.2.: Descriptive statistics (mean, median, SE) of the number and volume of sperm sacs. PWS - polyps with sperm sacs; N - number of observed sperm sacs; NSP - number of sperm sacs per polyp; VSP - volume of sperm sacs per polyp.

	Fertile polyps			**NSP** (sperm sacs polyp^{-1})			**VSP** (mm^3 polyp^{-1})		
	n	%	N	Mean	Median	SE	Mean	Median	SE
July 2009	50	100	1865	37.3	40.5	3.21	0.06752	0.05155	0.008950
September	50	100	2467	49.3	42.0	4.40	0.33579	0.29479	0.032329
October	41	82	156	3.8	2.0	0.71	0.01362	0.00045	0.003463
January 2010	45	90	85	1.9	1.0	0.24	0.00016	0.00013	0.000023
April	48	96	615	12.8	7.0	2.14	0.00656	0.00095	0.001865
July	50	100	2343	46.9	47.5	2.95	0.06764	0.04323	0.008792

5.3.5. Effects of colony and polyp size on fecundity

Colony size of the analysed female gorgonians presented some variation throughout the study period (Kruskal-Wallis' U test: $\chi^2_9 = 121.74,\ p < 2.2e^{-16}$), with lower values in July 2009 and June, January and March 2010 (multiple comparisons, $p < 0.001$). This was also observed for males (U test, $\chi^2_4 = 37.84,\ p = 1.11e^{-7}$), with July 2010 presenting larger colonies (multiple comparisons, $p < 0.001$). For each sampling date and for both sexes, the variation in the number of reproductive structures and their volume within each colony was greater than the variation between colonies. It was not detected an evident effect of colony size on the number of oocytes and spermaries and their volume. The size frequency distribution of oocytes or spermaries was not different between colonies of different sizes.

The equivalent diameter of polyps (proxy for polyp size) ranged from 580 to 1373 µm in females and 598 to 1433 µm in males. In August 2009, females presented larger polyps than in the remaining sampling dates (U test: $\chi^2_6 = 53.76,\ p = 8.23e^{-10}$). Nevertheless, the variation in polyp size was larger within individual colonies than between colonies. Significant positive linear correlations between polyp size and the number of oocytes were observed for two sets of samples (May-June and July-August) when production of new reproductive structures and maturation of pre-season oocytes was extremely active. However, these positive trends differed between dates: in May-June the effect of polyp size was lower ($y = -1.713 + 0.0163x$) and less evident ($r^2 = 0.217, F_{(1,98)} = 27.16, p < 0.001$) than in July-August ($y = -28.8421 + 0.0475x; r^2 = 0.603, F_{(1,148)} = 224.3, p < 0.001$). These trends were not dependent on colony size (ANCOVA, $p > 0.05$). However, oocyte volume was better predicted using a linear model with polyp size and colony size as predictors. In May-June ($r^2 = 0.538, F_{(2,97)} = 56.43, p < 0.001$) the effects of polyp size ($\beta = 2.94e^{-4}, t_{(97)} = 8.895, p < 0.001$) and height ($\beta = -3.27e^{-3}, t_{(97)} = -2.716, p < 0.01$) were significant. Similarly, in July-August, the multiple regression model $y = -0.399 + 4.376e^{-4}$ polyp size $+ 3.764e^{-3}$ height ($r^2 = 0.4162, F_{(2,147)} = 52.4, p < 0.001$) indicated polyp size ($t_{(147)} = 9.638, p < 0.001$) and colony height ($t_{(147)} = 2.597, p <$

0.05) as suitable predictors of the volume of oocytes. The size frequency distribution of oocytes and spermaries of different polyp size classes did not present significant differences, a pattern that was consistent along the sampling period.

5.3.6. Spawning and larval development

Sea surface temperature (SST) presented marked seasonality, with lower temperatures during winter (December to March: 14 to 17 °C) and a relatively large period with high SST during summer (June-October: 20 to 26 °C) (Figure 5.10). Chlorophyll *a*, used as proxy of phytoplankton, displayed the regular pattern for temperate waters, with a spring bloom (March-April) and a shorter secondary peak in autumn, presenting a high correlation with POC ($r = 0.894, t_{22} = 9.36, p < 0.001$). Radiation available for photosynthesis (PAR) was lower during winter (November-February).

Spawning was not observed in situ at any sampling period, but in September and October, small plumes of white milky substance were observed leaving the polyps when colonies were slightly squeezed. This phenomenon was not observed in all sampled colonies nor during other sampling periods. We hypothesize that these plumes were formed by spermatozoa because: 1) only a fraction of the colonies showed this behaviour; 2) the relatively large amount of substance leaving the polyps; 3) it was impossible to ascertain individual structures underwater (poor resolution as a result of their small size).

Production of new oocytes or spermaries and development of pre-season oocytes was more evident from May to September, coinciding with increasing SST. Ripening of female and male reproductive structures was highly synchronous, converging in August-September. In October, with decreasing SST, fecundity was significantly lower in both sexes (sperm sacs were reduced tenfold, Table 5.2) and mature reproductive structures were rare, indicating synchronous gamete release between sexes. Significant positive correlations between SST and both the number of mature oocytes (≥300 µm; $r = 0.82, t_{11} = 4.75, p = 0.006$) and oocyte volume ($r = 0.81, t_{11} = 4.65, p = 0.0007$) were registered. Both variables showed maximum values five to seven months after the highest concentrations of POC (lagged correlations; $r_{t-6} = 0.69$ for mature oocytes and $r_{t-7} = 0.66$ for oocyte volume). A peak in POC (and chlorophyll *a* occurred about two months after spawning (November-December).

Structures resembling gorgonian larvae were never observed inside polyps of either female or male colonies. The maturation of fertilized eggs occurring in mucus material adhering to the surface of gorgonians ("brooding" Coma et al., 1995) was never observed during sampling or elsewhere in southern Portugal. Furthermore, larvae crawling on parent colonies or nearby

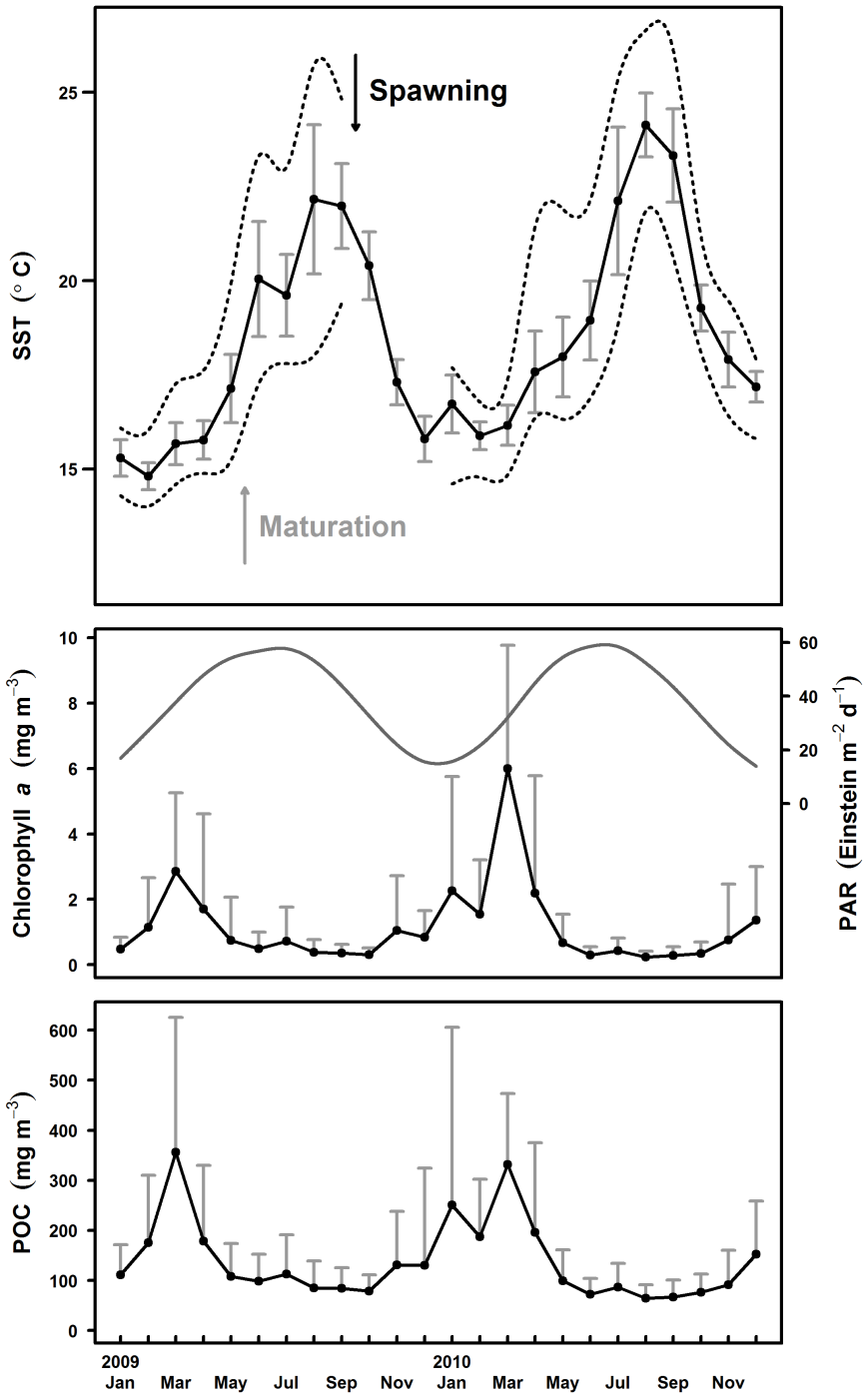

Figure 5.10.: Variation in sea surface temperature (SST), chlorophyll *a*, photosynthetically available radiation (PAR) and particulate organic carbon (POC) in southern Portugal during the study period (January 2009-December 2010).

sampled colonies were also never observed.

5.3.7. Loss of information on number and volume of reproductive structures

The number of oocytes counted under the stereo microscope predicted significantly the number of oocytes ($y = 4.442 + 1.175x, t_{(400)} = 40.84, p < 0.001$) as well as a significant part of the variance ($r^2 = 0.81, F_{(1,400)} = 1668, p < 0.001$). This trend was independent of the sampling date (ANCOVA, $p > 0.05$). The same pattern was observed for male colonies ($y = 4.182 + 1.537x, t_{(191)} = 6.402, p < 0.001; r^2 = 0.926, F_{(1,191)} = 2405, p < 0.001$) although the slope was significantly lower in September 2009 ($y = 2.298 + 1.231x, t_{(38)} = 6.402, p < 0.001; r^2 = 0.964, F_{(1,38)} = 1059, p < 0.001$).

5.4. Discussion

5.4.1. Sex ratio

The present study showed that *Eunicella gazella* is an iteroparous species with an annual reproductive cycle like several other temperate gorgonians, such as *Eunicella singularis* (Gori et al., 2007, ress; Ribes et al., 2007), *Eunicella verrucosa* (Munro, 2004), *Leptogorgia sarmentosa* (Rossi and Gili, 2009) and *Paramuricea clavata* (Coma et al., 1995; Gori et al., 2007). The observed sex ratio, not deviating significantly from parity, is similar to that reported for most species already studied (e.g. Coma et al., 1995; Orejas et al., 2002; Tsounis et al., 2006; Ribes et al., 2007). This pattern of balanced sex ratio is in accordance with optimal resource allocation in populations with random mating. However, biased sex ratios have been documented, both for females (e.g. Coffroth and Lasker, 1998; Ben-Yosef and Benayahu, 1999; Gori et al., 2007; Excoffon et al., 2011) or males (e.g. Brazeau and Lasker, 1992; Cerrano et al., 2005; Gori et al., 2007) (see also Table 5.3). Male biased sex ratios are supposed to increase fertilization success in gorgonians with brooding behavior (Benayahu and Loya, 1984b), by reducing sperm limitation effects (Levitan, 1993; Kahng et al., 2011). Because several octocoral species present oocytes all year round they are more likely to be identified, and this was suggested to be one of the reasons why female biased sex ratios in octocorals are quite common in the literature (Kahng et al., 2011).

5.4.2. Fecundity

Eunicella gazella presented large mature oocytes (Table 5.4). The observed values are slightly lower than those displayed by the internal brooder *Eunicella singularis*, but higher than those

reported for the broadcast spawner *Eunicella verrucosa* (Table 5.4). Even though large oocyte sizes (usually ≥600 µm) are usually found in species with internal fertilisation and brooding incubation mode (Orejas et al., 2002, and references therein), a recent review on the reproduction of octocorals found no relationship between oocyte size and reproduction mode; yet, species with extended oogenesis (over one year) have substantially larger oocytes than species with shorter oogenesis (Kahng et al., 2011). On the other hand, the fecundity of *Eunicella gazella* (number of mature oocytes per polyp) is within the highest values for the gorgonian species studied (Coma et al., 1995; Kahng et al., 2011; Torrents and Garrabou, 2011). Within the genus *Eunicella*, this is the highest fecundity ever reported, namely for *Eunicella singularis* (0.7–2.9 oocytes polyp^{-1}, Gori et al., 2007; Ribes et al., 2007) and *Eunicella verrucosa* (3.21–3.38 oocytes polyp^{-1}, Munro, 2004). Although sperm density may limit gorgonian reproductive success, it is the number of eggs produced that sets the upper limit for reproductive success (Beiring and Lasker, 2000).

Many factors have the potential to affect the fecundity of gorgonians, namely reproductive season (multiple spawnings or a seasonal mass event), depth, colony size and polyp position within the colony (e.g. Coma et al., 1995; Kapela and Lasker, 1999; Beiring and Lasker, 2000; Orejas et al., 2002). Due to their body morphology, polyp size is space-limited in gorgonians, and may limit gamete production (Coma and Lasker, 1997) as suggested for corals (Benayahu and Loya, 1984a). The current findings not only reinforce this idea, as there was a significant positive correlation between polyp size and fecundity in female colonies, but further suggest that the use of available space is optimized during the oogenic and spermatogenic cycles. In fact, when reproductive structures are at the final stages of maturation (August-September), the polyp cavity was completely occupied and the polyps presented a turgid appearance, in both male and female colonies. Moreover, new oocytes and sperm sacs develop beside or underneath older ones, thus achieving maximal space occupation. In *Eunicella gazella*, this is particularly important because the size of reproductive structures is relatively large considering its high fecundity.

The number of spermaries was 2-3 times higher of that of females, which corroborates previous studies on gorgonians (Coma et al., 1995; Tsounis et al., 2006; Ribes et al., 2007; Torrents and Garrabou, 2011), and may be related to the larger mean size of oocytes, or to other factors such as energy investment (Torrents and Garrabou, 2011). However, when reproductive structures are mature (September), estimates of their volume per polyp for females and males are not only similar between sexes, but also to those reported for other gorgonians (Tables 5.3 and 5.4). The volume of the reproductive structures within a species is related to fecundity, which may present spatial and depth related differences (e.g. Tsounis et al., 2006; Gori et al., 2007, ress; Torrents and Garrabou, 2011, see Tables 5.3 and 5.4). Volume in female and male colonies is similar during the maturation period in July-September, increasing fourfold (e.g. 3.9–16.7 mm^3, for 50 female polyps). However, after spawning in October, the volume decreased tenfold in females (1.6 mm^3, 50 polyps) and thirtyfold in males (0.5 mm^3, 50 polyps). This difference between sexes is because females retain

Table 5.3.: Information on the spermatogenic cycle of octocorals from the NE Atlantic and Mediterranean. Reproductive mode, sex ratio and mean values of spermaries volume, fecundity (mean±SD) and spermary size (mean±SD). IB - internal brooder; SB - surface brooder; BS - broadcast spawner

Species	Mode	Sex ratio	Male – *sperm sacs*				Depth	Locality	Geographic Area	Source
			Fecundity (polyp^{-1})	Volume (μm^3 polyp^{-1})	Size (μm)	Spawning				
		(F:M)					(m)			
SCLERAXONIA, Coralliidae										
Corallium rubrum	IB	1.37:1	6 ± 3.5	—	—	June	25-35	Ligurian Sea	Mediterranean	Santangelo et al. 2003
	IB	1:1	2.42 ± 0.166	—	476 ± 144	July	20-40	Costa Brava	Mediterranean	Tsounis et al. 2006
	IB	—	2.5 – 6.9	—	—	—	15-42	Marseille	Mediterranean	Torrents and Garrabou 2011
HOLAXONIA, Plexauridae										
Paramuricea clavata	SB	0.92:1	35 ± 6.1	—	326 ± 108[e]	June-July	17-19	Medes Islands	Mediterranean	Coma et al. 1995
	SB	1:1	24.3 ± 1.3[a]	6.60E+08		May-July	18-20	Medes Islands	Mediterranean	Gori et al. 2007
	SB	1:7	28.9 ± 1.3[a]	7.80E+08		June-September	30-35	Cape of Palos	Mediterranean	Gori et al. 2007
	SB	—	18.8 ± 11.38	—	—	—	20	Cap Creus[g]	Mediterranean	Tsounis et al. 2012
	SB	—	6.1 ± 8.30[b]	—	—	—	20	Cap Creus[g]	Mediterranean	Tsounis et al. 2012
	SB	—	25.0 ± 16.61	—	—	—	19	Cap Creus[h]	Mediterranean	Tsounis et al. 2012
	SB	—	6.4 ± 8.21[b]	—	—	—	19	Cap Creus[h]	Mediterranean	Tsounis et al. 2012
	SB	—	23.1 ± 15.54	—	—	—	19	Medes Islands[i]	Mediterranean	Tsounis et al. 2012
	SB	—	12.6 ± 12.23[b]	—	—	—	19	Medes Islands[i]	Mediterranean	Tsounis et al. 2012
HOLAXONIA, Gorgoniidae										
Leptogorgia sarmentosa	BS?	1.6:1	7.0 ± 2.8[c]	8.22E+07	254.3 ± 88.2[c]	August	30-32	Costa Brava	Mediterranean	Rossi and Gili 2009
Eunicella singularis	IB	1:1	13.6 ± 0.8[a]	2.60E+08	317 ± 1.9[a]	May-June	18-20	Medes Islands	Mediterranean	Gori et al. 2007
	IB	1.7:1	20.8 ± 0.8[a]	6.10E+08	426 ± 17.2[a]	June-July	30-35	Cape of Palos	Mediterranean	Gori et al. 2007
	IB	1.16:1	8.7	—	387 ± 106	May-June	15-20	Medes Islands	Mediterranean	Ribes et al. 2007
	IB	—	13.7 ± 1.5[a]	1.50E+08	340 ± 11[a]	May-June	20	Cap Creus	Mediterranean	Gori et al. ress
	IB	—	8.8 ± 1.0[a]	1.10E+08	304 ± 4[a]	May-June	60	Cap Creus	Mediterranean	Gori et al. ress
Eunicella verrucosa	BS	2:1	10.30 ± 2.87[d]	—	—	August-September	14-18	Skomer	NE Atlantic	Munro 2004
	BS	2:1	7.27 ± 5.23[d]	—	—	August-September	23	East Tennants Reef	NE Atlantic	Munro 2004
Eunicella gazella	BS	1.09:1	49.3 ± 31.14	3.30E+08	246 ± 117.9	September-October	16	Algarve	NE Atlantic	present study

[a] mature spermaries/polyp [b] cohort of mature oocytes [c] Mean ± Standard Error (SE) [d] impacted colonies [e] colony branch of order 3 [f] colony branch of order 2
[g] impacted by recreational fishing [h] impacted by recreational fishing and lobster pots [i] impacted by scuba diving

Table 5.4.: Information on the oogenic cycle of octocorals from the NE Atlantic and Mediterranean. Mean oocyte volume, fecundity (mean±SD) and oocyte size (mean±SD). Oocyte size range before spawning is also presented.

Species	Female – *oocytes*					Depth	Locality	Geographic Area	Source
	Fecundity (polyp^{-1})	Volume (μm^3 polyp^{-1})	Size (μm)	Range	Spawning	(m)			
SCLERAXONIA, Coralliidae									
Corallium rubrum	2.3 ± 0.3	—	—	—	June-July	25-35	Ligurian Sea	Mediterranean	Santangelo et al. 2003
	0.66 ± 0.024[a]	—	418 ± 178	500-900	July-August	20-40	Costa Brava	Mediterranean	Tsounis et al. 2006
	1.0 – 3.2	—	—	—	—	15-42	Marseille	Mediterranean	Torrents and Garrabou 2011
HOLAXONIA, Plexauridae									
Paramuricea clavata	13 ± 2.2	—	425 ± 76[e]	—	June-July	17-19	Medes Islands	Mediterranean	Coma et al. 1995
	11.6 ± 0.6[a]	2.90E+08	398 ± 4.7	200-550	May-July	18-20	Medes Islands	Mediterranean	Gori et al. 2007
	27.9 ± 2.0[a]	5.80E+08	352 ± 3.3	200-550	May-July?/August?	30-35	Cape of Palos	Mediterranean	Gori et al. 2007
	17.3 ± 10.00	—	—	—	—	20	Cap Creus[g]	Mediterranean	Tsounis et al. 2012
	8.6 ± 5.80[b]	—	—	—	—	20	Cap Creus[g]	Mediterranean	Tsounis et al. 2012
	14.4 ± 6.61	—	—	—	—	19	Cap Creus[h]	Mediterranean	Tsounis et al. 2012
	0.5 ± 1.42[b]	—	—	—	—	19	Cap Creus[h]	Mediterranean	Tsounis et al. 2012
	10.7 ± 10.72	—	—	—	—	19	Medes Islands[i]	Mediterranean	Tsounis et al. 2012
	9.6 ± 13.66[b]	—	—	—	—	19	Medes Islands[i]	Mediterranean	Tsounis et al. 2012
HOLAXONIA, Gorgoniidae									
Leptogorgia sarmentosa	4.3 ± 1.9[f*]	1.88E+07	162.7 ± 84.2[f*]	—	September?	30-32	Costa Brava	Mediterranean	Rossi and Gili 2009
Eunicella singularis	2.9 ± 0.2[a]	2.50E+08	413 ± 18.1[a]	300-900	May-June	18-20	Medes Islands	Mediterranean	Gori et al. 2007
	4.5 ± 0.2[a]	2.90E+08	465 ± 13.5[a]	300-900	June-July	30-35	Cape of Palos	Mediterranean	Gori et al. 2007
	0.69 ± 0.16[d]	—	615 ± 130[e]	450-860	May-July	15-20	Medes Islands	Mediterranean	Ribes et al. 2007
	5.1 ± 0.5[a]	1.30E+08	351 ± 40[a]	300-900	May-July	20	Cap Creus	Mediterranean	Gori et al. ress
	5.3 ± 0.9[a]	9.60E+07	300 ± 5[a]	300-900	May-June	60	Cap Creus	Mediterranean	Gori et al. ress
Eunicella verrucosa	3.21 ± 3.60[d]	—	—	—	August-September	14-18	Skomer	NE Atlantic	Munro 2004
	3.38 ± 4.24[d]	—	—	—	August-September	23	East Tennants Reef	NE Atlantic	Munro 2004
Eunicella gazella	27.3 ± 13.24	3.30E+08	490 ± 77.6[e]	350-776	September	16	Algarve	NE Atlantic	present study
	9.1 ± 4.60[d]								

[a] mature oocytes/polyp [b] cohort of mature oocytes [c] Mean ± Standard Error (SE) [d] impacted colonies [e] colony branch of order 3 [f] colony branch of order 2
[g] impacted by recreational fishing [h] impacted by recreational fishing and lobster pots [i] impacted by scuba diving

small oocytes for the next reproductive season.

In general, fecundity increases with colony size in octocorals (e.g. Benayahu and Loya, 1984a; Coma et al., 1995; Kapela and Lasker, 1999), and within a population large colonies sometimes contribute disproportionately to egg production (Coma et al., 1995; Beiring and Lasker, 2000). Increasing fecundity with size may result from an increased number of polyps per colony, as well as an increase in the reproductive output at the polyp level (Beiring and Lasker, 2000), possibly as a consequence of a shift in resource allocation from growth to reproduction once the colony has reached a size-refuge threshold (Beiring and Lasker, 2000). Colony size effect was not verified in the present work, but sampling variation may be masking this effect. Therefore, further studies with appropriate replication, performed in a narrow period of time but comprising a broad range of colony sizes should clarify if the observed pattern was biased due to sampling. In the present study, a positive relationship between fecundity and polyp size was observed at all sampling periods, suggesting that variability in polyp size may be responsible for considerable variation in fecundity, especially considering that the apical position within the colony was fixed, thus removing one source of error associated to differences in fecundity within octocoral species. For some coral species, polyp volume in medium and large sized colonies is similar, even though large colonies have more polyps (Sakai, 1998). A recent study with *Astroides calycularis* reported a logarithmic relationship between the number of polyps and both colony length and width, but a linear relationship with colony area and mass (Goffredo et al., 2011). In addition, large colonies had polyps with smaller size than small and medium colonies, due to an over-representation of the size class containing sexually mature polyps, suggesting that large colonies may invest energetic resources to increase the size of young polyps up to the size at sexual maturity, rather than increasing the size of already mature polyps (Goffredo et al., 2011). This agrees with the size threshold that may lead to differences in energy allocation from growth to reproduction (Sakai, 1998). Indeed, energy investment in reproductive tissue increases in corals with larger polyps, but the gonadosomatic index decreases, suggesting polyp size constraints (Sakai, 1998). This change in energy allocation from growth-dominated to reproduction-dominated with increasing colony size, is based on the assumption that reproduction comes at the expense of growth, so it is possible that age and not colony height would be a better correlate with polyp fecundity (Pakes and Woollacott, 2008).

In corals, large-scale spatial and temporal variation in recruitment is clearly linked to patterns of variation in fecundity rather than adult abundance (Hughes et al., 2000). However, a negative correlation between polyp fecundity and population density has been suggested for benthic cnidarians (Orejas et al., 2002). The present study was conducted in a area where *Eunicella gazella* is very frequent and dominant in terms of density (13.2 colonies/5m^2) (Cúrdia et al., 2sub), although presenting high fecundity. Additional studies in contrasting density levels shall provide further insights on this subject. The present study showed that *Eunicella gazella* favours

a reproductive strategy with high number of relatively large oocytes and synchronized spawning to ensure that oocytes are fertilized (probably in the area), which also provides a relatively high dispersal potential (large oocytes) to colonize adjacent areas with lower density or under lower competitive pressure. In fact, it has been proved that coral larvae are distributed relatively uniformly among adjacent reefs, but do not undergo larger-scale movements, resulting in modest gene-flow in spawning corals (Hughes et al., 2000). *Eunicella gazella* is original from tropical areas but, apparently, expanded recently its distribution to northern latitudes probably because of favourable conditions under a global warming scenario. The broadcast spawning behaviour of this species, contrasts with the brooding behaviour of *Eunicella singularis* and *Eunicella cavolinii*, the most common *Eunicella* species in the Mediterranean, and seems to be efficient, as *Eunicella gazella* is frequent and density dominant in southern Portugal (Cúrdia et al., 2sub). Moreover, the populations present numerous small sized colonies (Cúrdia et al., 2sub), suggesting that recruitment events are frequent and successful. In contrast, *Eunicella singularis* is extremely rare and *Eunicella cavolinii* has never been found in southern Portugal, whereas the broadcast spawner *Eunicella verrucosa* (Munro, 2004), has been recently reported to be expanding its distribution in the Mediterranean (Sartoretto and Francour, 2012) and is frequent in southern Portugal (Cúrdia et al., 2sub). Differences in spawning mode may alter fertilization and recruitment success of gorgonian species and consequently constrain population dynamics. To what level, under the complex variety of factors acting on coastal areas, one mode is more successful than the other remains an important but decisive question yet to be fully addressed.

5.4.3. Spawning

The longer duration of oogenesis compared to spermatogenesis, is a common feature of the reproductive development in gorgonians (Coma et al., 1995; Tsounis et al., 2006; Ribes et al., 2007; Gori et al., ress), but also the general pattern for octocorals (Benayahu and Loya, 1984a), alcyonaceans and many scleractinians (Szmant, 1986). Several octocoral species keep immature oocytes year-round, with a fraction maturing during a seasonal oogenic cycle, as for instance *Acabaria biserialis* (Ben-Yosef and Benayahu, 1999), *Eunicella singularis*, (Ribes et al., 2007; Gori et al., ress) and *Tripalea clavaria*, (Excoffon et al., 2004, 2011). This pattern is consistent with the theory that oogenesis is more energetically expensive than spermatogenesis (Kahng et al., 2011). On the other hand, in order to achieve synchronous spawning in both sexes, and thus to minimize the loss of gametes (Grosberg and Levitan, 1992; Lasker and Kim, 1996; Carlon, 1999; Ritson-Williams et al., 2009), spermatogenesis has to be delayed (Coma et al., 1995; Tsounis et al., 2006; Gori et al., 2007, ress). The fact that spermatogenesis took longer than commonly found in other octocorals may be because the quantification of spermaries was undertaken in a microscope, instead of a stereo microscope. High fecundity and volume of reproductive structures in both sexes suggests that *Eunicella gazella* invests a lot of energy on sexual reproduction, a common strategy

in other gorgonian species (Coma et al., 1995, 1998; Ribes et al., 2007; Linares et al., 2008a; Gori et al., ress; Tsounis et al., 2012). Energy investment (i.e. volume of oocytes or spermaries) seems to be similar in both sexes, but males produce more structures. Therefore, it is possible that by increasing the production of male gametes, *Eunicella gazella* is enhancing fertilization likelihood, as pointed by Coma et al. (1995) for *Paramuricea clavata*. The maximum size of mature oocytes is similar to those reported for other gorgonian species. Considering the high fecundity registered, the investment in large oocytes (increasing longevity and allowing energy reserves for the zygote) may be a strategy to improve fertilization success through increased sperm-egg encounter rates (Levitan, 1993), favouring broadcasting mode.

The investment in offspring is generally related to environmental conditions, being larger in less stable regions (e.g. temperate waters). Some studies mentioned that several gorgonians require a peak summer temperature above a certain threshold as a cue for spawning (Coma et al., 1995; Gori et al., 2007; Pakes and Woollacott, 2008; De Putron and Ryland, 2009) and that temperature is the main factor synchronizing the development of reproductive structures (Gori et al., 2007). Long-lived species with slow oocyte development, such as octocorals, in areas with marked but predictable seasonal variation in food availability, tend to present gametogenic cycles that follow such variations (Coma et al., 1998; Gori et al., 2007, ress; Ribes et al., 2007, and references therein). Spatial and depth differences in the timing of spawning of gorgonian species have been attributed to differences in sea surface temperature, which may also be the reason why the spawning in *Eunicella gazella* is delayed compared to *Eunicella singularis* in the Mediterranean (Gori et al., 2007; Ribes et al., 2007) and *Eunicella verrucosa* in the United Kingdom (Munro, 2004). Even though the feeding habits of this species are unknown, temperate gorgonians feed mainly on zooplankton (copepods and nauplii) and POM (Coma et al., 1994; Ribes et al., 2003; Tsounis et al., 2005). For example, in the Mediterranean, *Paramuricea clavata* shows higher energy allocation for reproduction in March-June, when ingestion rates coupled with the spring bloom are higher, but also presents increased feeding rates in November-December during the shorter autumn bloom (Coma et al., 1998). The energy surplus during periods of high food availability (winter and spring) are invested in secondary production (Coma et al., 1998). Similar models have been proposed for other gorgonian species feeding primarily on microzooplankton and POM (Ribes et al., 2007; Gori et al., 2007, ress). Therefore, it is expectable that the reproductive cycle of *Eunicella gazella* should also be regulated by food availability. After the spring bloom (March-April), *Eunicella gazella* transfers the energy surplus to the intensive production and maturation of oocytes and spermaries, enhanced by the high summer temperatures, ending the cycle with the synchronised spawning by female and male colonies in September-October. The occurrence of a second phytoplankton bloom, and the frequent upwelling conditions, provide a relatively prolonged period of increased chlorophyll *a* and POC concentrations during autumn-winter. The fact that spawning occurs immediately before this period of increased food availability suggests that this energetic surplus is crucial in the reproductive strategy of this species. Feeding and energetic studies may help to

discern how *Eunicella gazella* uses the autumn bloom. According to the present study, production of new oocytes is not increased and sperm sacs are vestigial during this period, and the small oocytes that were kept after spawning do not show signs of continuous maturation. The planulae of gorgonians with broadcast spawning usually take 4 to 15 days to settle (Table 3; Linares et al., 2008, and references therein), therefore increased food in autumn can be used by the recruits to enhance the initial phase after settlement.

5.4.4. Conservation issues and knowledge gaps

A trade-off between regeneration and reproduction has been reported for different coral species (Szmant, 1990; Van Veghel and Bak, 1994; Rinkevich, 1996; Ward et al., 2000), namely gorgonians (Linares et al., 2008a; Tsounis et al., 2012). Fecundity may be reduced in damaged parts of the colony, but can also be extended far from the damaged area (Linares et al., 2008a). As a result, besides their immediate impacts, disturbance events may also present delayed effects on the reproductive output of gorgonian species, therefore, affecting their long-term recovery (Tsounis et al., 2006, 2012; Linares et al., 2008a). The samples analysed in the present study were collected in an area under high fishing pressure (Cúrdia et al., 2sub) and a significant part of *Eunicella gazella* population presents tissue damage and consequent fouling by other biota (unpublished data). However, colonies presenting signs of damage or extensive fouling were not collected, in order to avoid introducing bias in this study on the reproductive cycle. Nevertheless, it is important to compare the present data with that obtained in areas without or under lower pressure that can affect this gorgonian species. Moreover, the correlation between damage and fecundity should be analysed in colonies from the same population, under similar environmental conditions. Spatial and temporal variations in fecundity should also be estimated for the area.

In the near future, the present study shall be complemented with studies performed during the spawning period, with short intervals between samples, aiming to confirm the broadcasting behaviour and test the existence (and frequency) of brooding in this species. In addition, researchers should develop specific sampling techniques to allow identifying larvae on/or in the vicinity of colonies. The use of specifically designed collectors can also shed light on the type of spawning. Recruitment studies are also of utmost importance to understand how the larval supply is used in the area, and what are the consequences for the dynamics, gene flow, and ultimately persistence of the species along time. The present data disclosed the general reproductive cycle of *Eunicella gazella*, providing baseline information for future studies focusing directly or indirectly on the reproduction of this habitat engineering long-lived suspension feeder.

Acknowledgements

The authors would like to thank to Pedro Lino, Marco Cerqueira and Susana Carvalho for their help during sample collection and processing, and to Paula Moura for the help on histological procedures. The first author benefits from a PhD grant (SFRH/BD/29491/2006) awarded by the Fundação para a Ciência e a Tecnologia (FCT). The MODIS mission scientists and associated NASA personnel are also acknowledged for producing the satellite remote sensing data (chlorophyll *a* concentration, PAR and POC) used in this study.

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Part IV.

Human pressures in the Algarve sublittoral rocky bottoms

CHAPTER 6

Scuba divers' profile and their impacts on the benthic environment: a contribution for the management of multiuse coastal areas

Submitted to: *Scientia Marina*

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Abstract

In south Portugal, scuba diving is growing, following the worldwide pattern. The preference of scuba divers for natural rocky areas with diverse fauna put these habitats under threat. The assessment of the impacts and their causes is therefore an important issue for the management of coastal areas, particularly if they face multiple uses. In 2005-2007, during the summer season when scuba diving is more intense, 105 scuba divers were monitored while diving. Their behaviours, the consequences of their actions and the associated impacts were recorded to estimate the impact of scuba divers in the habitat. Most of the scuba divers (88.6 %) showed behaviours that may impact marine systems and the mean contact rate was 0.340 ± 0.028 contacts min^{-1}. The rate was higher in scuba divers with moderate experience, and in the initial part of the dive (0–10 min). Contacts with fins and hands dominated, mainly resulting in sediment re-suspension, but the estimated impacts associated were generally low. However, fauna was also affected by physical damage and interactions, which may severely impact animals, especially suspension feeding sensitive species such as gorgonians. Based on the observed patterns, some ideas are discussed in order to reduce scuba diving impacts at local and global scales.

Keywords: Scuba diving • impact • diver's experience • natural versus artificial habitats

6.1. Introduction

Scuba diving is a growing activity worldwide (Davis and Tisdell, 1995; Harriott et al., 1997; Barker and Roberts, 2004; Davenport and Davenport, 2006). Mainland Portugal has attractive conditions for the development of this recreational activity, especially in its southern coast, the Algarve, that showed in the recent years a sharp increase in the number of dives, certified divers and scuba diving centres (Santos et al., 2006). The Algarve region presents an offer of tourism-related products of excellence and natural conditions for sport tourism, and therefore in the near future the activity is expected to grow (Santos et al., 2006) as the local authorities are fostering the diversification of tourism products, especially expanding activities that can be certified as "environmentally friendly" and sustainable (Correia and Pires, 2006; Pires, 2008).

Scuba divers prefer and are willing to pay more to dive in sites with high biological diversity, high abundance of certain species (mainly fish) and high probability to observe large animals (Rudd and Tupper, 2002; Green and Donnelly, 2003; Dearden et al., 2007). In this context, habitats with complex biological communities, significant ecological importance and a strong contribution for marine biodiversity such as rocky areas in tempered waters, especially in marine protected

areas (MPAs) (Milazzo et al., 2002; Coma et al., 2004; Luna et al., 2009) and coral reefs in tropical and subtropical waters are highly demanded. Coral habitats in particular suffer high intensity of diving, especially in the Red Sea (>250 000 dives yr^{-1} in Eilat, 12 km of coast; >30 000 dives yr^{-1} in Dahab; 20 000 dives yr^{-1} per mooring buoy in Ras Mohammed National Park Medio et al., 1997; Zakai and Chadwick-Furman, 2002; Hasler and Ott, 2008)), the Grand Barrier Reef in Australia (10 000–20 000 dives yr^{-1} Harriott et al., 1997) and the Caribbean (5000–6000 dives yr^{-1} Hawkins et al., 1999). The rapid growth of scuba diving led to increasing concerns of the impacts of the activity all over the world (Medio et al., 1997; Jameson et al., 1999; Tratalos and Austin, 2001; Coma et al., 2004) which adds to other existing threats. Rocky areas in tempered waters are also impacted by many disturbance factors, mostly related to human activities such as urban development, fishing and recreational activities (Crowe et al., 2000; Milazzo et al., 2002; Lloret and Riera, 2008), while coral reefs are severely threatened by overfishing, pollution, climate change and ocean acidification (e.g. Hughes et al., 2003; Hoegh-Guldberg, 2010; Pandolfi et al., 2011), leading to phase shifts, spread of diseases and decline of the high biodiversity typical of these habitats (e.g. Knowlton, 2001; Hughes et al., 2007; Plaisance et al., 2011).

Several studies were conducted to identify the impacts and calculate the carrying capacity of intensively used dive sites (e.g. Davis and Tisdell, 1995; Medio et al., 1997; Hawkins et al., 1999; Zakai and Chadwick-Furman, 2002; Barker and Roberts, 2004). Even though considered an "ecofriendly" activity, several impacts have been identified and associated to scuba diving leading to the degradation of marine ecosystems (e.g. Harriott et al., 1997; Zakai and Chadwick-Furman, 2002; Barker and Roberts, 2004; Coma et al., 2004; Luna et al., 2009). In coral reefs, the coral cover decreased in intensively dived areas due to total or partial mortality (Rouphael and Inglis, 1997; Hawkins et al., 1999; Jameson et al., 1999; Tratalos and Austin, 2001; Zakai and Chadwick-Furman, 2002; Hasler and Ott, 2008; Leujak and Ormond, 2008; Hannak et al., 2011). Although studies to assess the impacts of scuba diving in temperate waters are scarce (Garrabou et al., 1998; Coma et al., 2004; Di Franco et al., 2009; Luna et al., 2009), damage in species characteristic of pre-coralligenous, coralligenous and sciaphilous habitats have been found to be significant (Coma et al., 2004; Luna-Pérez et al., 2010). Mitigation measures to reduce or alleviate those impacts have been frequently suggested, constituting important tools for the management of dived areas (protected or not).

In the Algarve, shallow water subtidal rocky areas present a rich benthic community (Gonçalves et al., 2007, 2010), with a mixed assemblage of gorgonian species standing out as important habitat formers and the most conspicuous fauna. These gorgonian gardens that enhance local biodiversity by harbouring a rich and diverse associated fauna (Carvalho et al., sub.) extend to deeper waters and have been recently proposed to be included in OSPAR's protected habitats (Anonymous, 2011).

Rocky areas with gorgonian gardens are attractive seascapes very popular among scuba divers

(Rodrigues, 2008) and are therefore prone to impacts resulting from such activity. Also, dived areas, such as the Algarve coast, commonly serve multiple purposes such as fishing and boating, and are often the subject of stakeholders' conflicting interests. To properly manage multi-use areas it is important to understand and quantify the impacts of each use, namely scuba diving, in order to build management plans to restore the impacted areas and achieve a balance between preservation of biodiversity and resource utilization. The main goal of this study is to assess the impact of scuba diving in the Algarve coast. Specific objectives are: i) estimate the rate of scuba divers' actions according to their diving experience; ii) to determine whether the rate of actions is similar along different diving time frames (10 min and 10–30 min); iii) to identify the main actions performed by the scuba divers that interact with the environment and their immediate consequences; and, iv) compare scuba divers' behaviour on rocky areas and wrecks. The identification and quantification of the main actions and their consequences will be discussed considering their estimated impacts and strategies will be pointed out to prevent those actions and minimize their consequences. Conservation measures will be proposed and discussed according to the main facts observed.

6.2. Materials and Methods

6.2.1. Study area

The Algarve presents a large diversity of features within its coastal zone, from rocky cliffs surrounding small bays to large sandy beaches with low slope and small scattered rocky areas or submerged fossilized ancient dunes. Furthermore, there are a few wrecks with differing ages that currently are used for scuba diving. The entire coastal zone is subjected to several anthropogenic pressures, namely urban development for housing and tourism, intensive use of the areas for recreational activities, boating and both sport and commercial fishing, the latter with a wide range of fishing gears and techniques. The coastal zone of the Algarve is very productive due to seasonal upwelling and its marine communities are rich and diverse, benefiting from the convergence of waters from different regions, namely the Mediterranean Sea, the North Atlantic and the Northwest coast of Africa (Cherubin et al., 2000; Martins et al., 2002; Souto et al., 2010; Levy et al., 2011). Moreover, there are important transitional systems in the Algarve, namely estuarine-lagoon systems such as the Ria de Alvor and the Guadiana and barrier islands such as the Ria Formosa (Carvalho et al., in press) which have been extensively studied and proven to be important nursery areas (Abecasis et al., 2009; Vasconcelos et al., 2010, 2011). Despite the ecological relevance of the region, marine reserves have not yet been established in the Algarve coast and the strategy for marine species and habitats protection is based on the Habitats Directive and Natura 2000.

6.2.2. Sampling strategy

In order to estimate the impact of recreational scuba diving in the Algarve coast, scuba divers were monitored underwater. The samples were collected during regular scuba diving trips of three diving centres that participated in the study and are representative of the offer in the region. The 23 diving sites that were considered fall into two different categories, rocky areas (subtidal rocky bottoms; 19 sites) and wrecks (shipwrecks and a World War II downed airplane; 4 sites). These categories are representative of the Algarve diving areas with much more rocky sites than wrecks (Santos et al., 2006). Between 2005 and 2007, during the summer, 120 dives were monitored, but only 105 of them proved to have the necessary requirements to be analysed with no bias, 76 in rocky areas and 29 in wreck areas.

All underwater surveys were carried out by the same two observers (J. Cúrdia and M. Ferreira). Preliminary surveys were performed to define sampling strategy, set the criteria for actions, consequences and impacts, and to check sampling consistency. These surveys indicated that it was impracticable to record the exact timing of each action, therefore two time frames were defined: the first 10 min of the dive (starting from the moment that the scuba diver reached the seafloor and started the recreational dive) and the following 10–30 min. It was also defined that after the 30 min of dive, the contacts, actions, consequences and impacts continued to be monitored until the end of the recreational dive (i.e. whenever the dive leader or any of the dive buddies declared that the dive had finished and divers should start to ascend) and the total dive time was annotated. Furthermore, because of local oceanographic conditions, namely reduced visibility, each observer was only able to monitor one or two different divers in each dive. The sets of data from both observers after some dives were found to be very similar, allowing the comparison of data collected by both observers, assuming negligible bias. The criteria used in assessing the impacts were set according to the preliminary surveys and published information (Figure 6.1). The actions that were ranked as having higher impact were those that introduced any kind of stress to animals, or significantly harmed the biological entities or its habitat. The actions that produced no observable consequence were rated as low impact actions.

Information regarding the experience and certification level of the scuba divers was collected by informally inquiring scuba divers and diving centres' staff. Three levels of diving experience were defined: low (less than 20 dives), moderate (20–50 dives) and high (more than 50 dives). During pre-dive briefing all the scuba divers in each diving trip were informed that the observers were conducting surveys to identify marine fauna and therefore would take notes during the dive. For each diver the actions and behaviours were recorded, as well as the immediate consequence of the scuba diver action. The impact of the consequence was assessed "in situ" in real time according to the previously set of criteria (Figure 6.1). In the post-dive, generally, the scuba divers were curious about the number of species identified and whether they have seen the same species. The

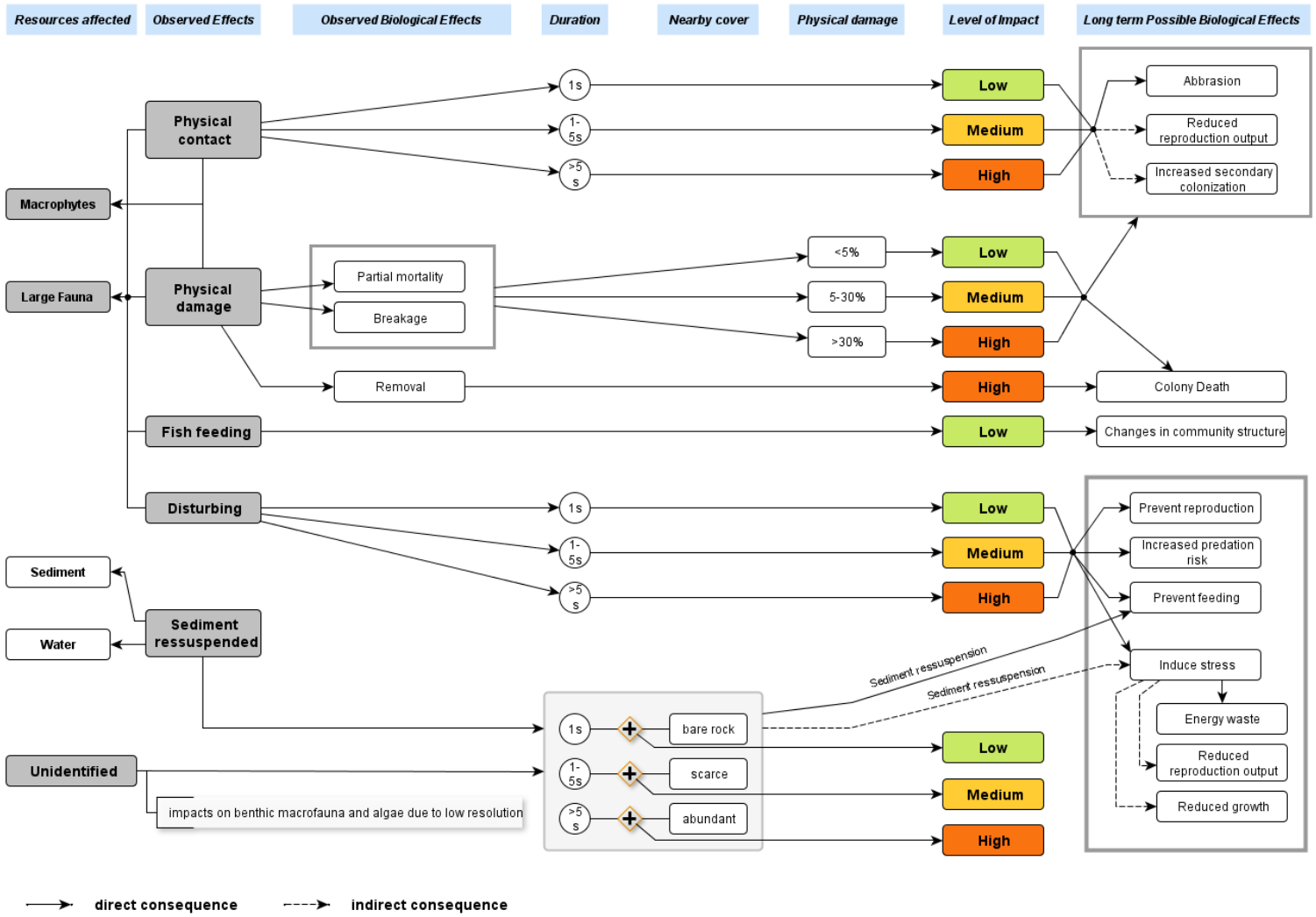

Figure 6.1.: Set of criteria used to rate the impacts of scuba divers. The three levels of impact were mainly distinguished by the duration of the contact or behaviour (physical contact and disturbing fauna) or the extension of the physical damage (percent area affected). For sediment re-suspension and undetermined effects the both the duration of the contact and the benthic cover were used. Only one case of fish feeding consisting of two small fish, therefore rated as low impact. The physical removal of sessile colonies (gorgonians, sponges, bryozoans were always considered as presenting high impact as they lead to colony death. The possible biological effects are based on published information regarding different taxonomic groups.

observers described briefly the main observed species and alerted for extra caution, especially towards some focal species, and for the correct behaviour while diving (e.g. avoid the interaction with species, no feeding). Due to diving constraints (divers got lost, gear malfunction, etc...) some dives were not used for the analysis as they were significantly biased. Divers that got aware of the observers' purposes were also excluded from the analysis. The 105 dives used in the current work all correspond to valid samples.

6.2.3. Statistical analyses

Contact rates were defined in the present work as the number of contacts performed by the scuba diver in a determined period of time. The different time frames sampled have different (and variable) duration (10 min, 20 min, 0–30 min), therefore data was standardised for time units (i.e. contacts min^{-1}). Contact rates data did not show a normal distribution (Kolmogorov-Smirnov test), consequently non-parametric tests were used to test the significance of the differences between groups of samples. The contact rates for different experience levels were compared for each diving site category (rocky areas vs. wrecks) using the Wilcoxon signed-ranks test (paired tests). For the contact rates of different periods of the dive (initial 10 min, 10–30 min, block data) the Friedman test was used (Legendre and Legendre, 1998; Barker and Roberts, 2004).

6.3. Results

6.3.1. Scuba diver characterization

In the present work, the study subjects (divers) were generally men (81.6 %, significant deviance from the a 0.5 ratio, $p < 0.001$, binomial test). Most divers were between 20–40 yr old, and only a few subjects were more than 50 yr old. Samples included tourists visiting the Algarve, both national and international visitors, and local scuba divers, mostly regular customers of the diving centres. National citizens accounted for 67.0 % of the studied subjects, a percentage that does not agree with the expected ratio for Algarve (4 Portuguese: 6 Foreigner, unpublished data; $p < 0.001$, binomial test) based on data gathered from unofficial enquiries (Santos et al., 2006). The logistic constraints (64 dives in Faro, 22 dives in Vilamoura and 18 dives in Lagos) may have also influenced these numbers as the diving centre from Lagos estimates that around 95 % of their divers are from foreign countries, whereas the other two centres, estimate around 10 % (Faro) and 50 % (Vilamoura). Nevertheless, the authors are convinced that the used dataset is representative of the scuba diving market in the Algarve typically with a strong spatial and seasonal variation (Santos et al., 2006).

6.3.2. Scuba diver's interactions

Overall, 93 of the 105 observed divers (88.6 %) made one or more contacts during their dive. From the 93 divers with contacts, 34 of them made up to 5 contacts in a single dive, and 55 made 10 or less contacts. However, 37 divers presented between 11and30 contacts and one scuba diver presented 54 contacts in a single dive (60 min). Overall, the mean contact rate was 0.340 ± 0.028 contacts min^{-1} ($\pm$SE) and the median was 0.27 contacts min^{-1}. The distribution of contact rates at rocky areas and wrecks was not normally distributed (Kolmogorov-Smirnov test, $p < 0.05$) but skewed towards low rates (skewness, 0.92 and 1.21, respectively) consistently resulting in lower median values than the mean contact rates at both dive site types (Table 6.1). Most of the divers made contacts, independently of dive site type (rocky areas and wrecks) and experience level (low, moderate and high experience) (Figure 6.2).

Table 6.1.: Contact rates for rocky and wreck scuba divers in the Algarve, discriminated by experience and time of the dive. SWC - samples with contacts; SE - standard error; Q_1 - first quartile; Q_3 - third quartile; max - maximum contact rate

Dive site type	Sampling period	Experience	NºSamples	SWC		Median	SE median	Q_1	Q_3	Mean	SE	max
Rocky	Entire dive	Low	28	23	82.1%	0.23	0.067	0.10	0.44	0.33	0.062	1.20
		Moderate	19	15	78.9%	0.30	0.132	0.04	0.58	0.36	0.075	0.90
		High	29	28	96.6%	0.25	0.079	0.08	0.45	0.27	0.041	0.76
			76	66	86.8%	0.25	0.033	0.08	0.48	0.32	0.033	1.20
	0–10 min	Low	28	20	71.4%	0.40	0.136	0.00	0.80	0.41	0.078	1.30
		Moderate	19	14	73.7%	0.60	0.212	0.05	0.90	0.56	0.121	1.50
		High	29	25	86.2%	0.40	0.094	0.10	0.60	0.38	0.052	0.90
			76	59	77.6%	0.40	0.096	0.10	0.70	0.44	0.046	1.50
	10–30 min	Low	28	23	82.1%	0.15	0.053	0.09	0.47	0.29	0.058	0.95
		Moderate	19	14	73.7%	0.25	0.093	0.05	0.45	0.31	0.073	1.25
		High	29	22	75.9%	0.15	0.063	0.05	0.45	0.23	0.040	0.65
			76	59	77.6%	0.15	0.046	0.05	0.45	0.27	0.032	1.25
Wrecks	Entire dive	Low	6	5	83.3%	0.17	0.144	0.10	0.36	0.24	0.097	0.63
		Moderate	13	13	100.0%	0.37	0.109	0.13	0.43	0.36	0.075	1.00
		High	10	9	90.0%	0.13	0.055	0.08	0.24	0.18	0.052	0.57
			29	27	93.1%	0.17	0.065	0.10	0.40	0.27	0.044	1.00
	0–10 min	Low	6	4	66.7%	0.25	0.350	0.03	0.85	0.42	0.194	1.00
		Moderate	13	12	92.3%	0.50	0.146	0.20	0.70	0.49	0.085	1.00
		High	10	6	60.0%	0.15	0.087	0.00	0.28	0.16	0.052	0.40
			29	22	75.9%	0.30	0.089	0.10	0.60	0.36	0.062	1.00
	10–30 min	Low	6	5	83.3%	0.13	0.117	0.05	0.31	0.18	0.075	0.45
		Moderate	13	10	76.9%	0.05	0.052	0.05	0.25	0.13	0.042	0.45
		High	10	8	80.0%	0.13	0.069	0.06	0.25	0.20	0.067	0.70
			29	23	79.3%	0.10	0.032	0.05	0.25	0.17	0.033	0.70

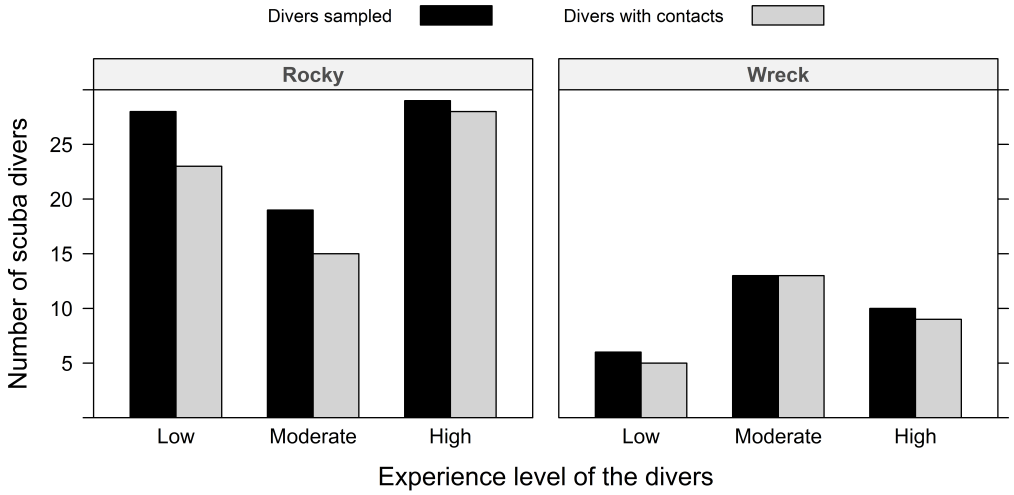

Figure 6.2.: Number of scuba divers showing contacts in relation to the total number of sampled scuba divers discriminated by diving experience for rocky areas and wrecks.

6.3.3. Factors influencing the rate of contacts

In general, the rate of contacts by scuba divers was higher in the initial part of the dive (10 min) than in the middle/final part of the dive (Table 6.1 and Figure 6.3). In fact, of the 105 divers analysed only 19 increased the number of contacts after the initial 10 min of the dive, most of them presenting low contact rates (13 divers under 0.2 contacts min^{-1}.)

In rocky areas, moderate and high experience divers, showed significantly higher contact rates in the initial 10 min of the dive (Friedman test, $\chi^2 = 7.14$, $p < 0.01$ and 17.19, $p < 0.001$, respectively; Table 6.1 and Figure 6.3). Noteworthy, in the initial 10 min of the dive in rocky areas, high experience divers showed the lowest rates (0.40 contacts min^{-1}) whereas the highest rates (0.60 contacts min^{-1}) were from moderate experience divers.

In the wreck areas, the contact rates were generally higher in the initial part of the dive (10 min) for all experience levels. However, contact rates were only significantly higher in the initial part of the dive (10 min) for moderate experience divers (Friedman test $\chi^2 = 6.23$, $p < 0.05$; Table 6.1 and Figure 6.3). For low and high experience levels, the differences between contact rates were not found significant, because of the small number of samples (low power of the test) and the high variability in wrecks' data. Similarly to rocky areas, high experienced divers presented the lowest rates (median 0.15 contacts min^{-1}) and moderate experienced divers the highest rates (median 0.50 contacts min^{-1}) in the first 10 min of the dive.

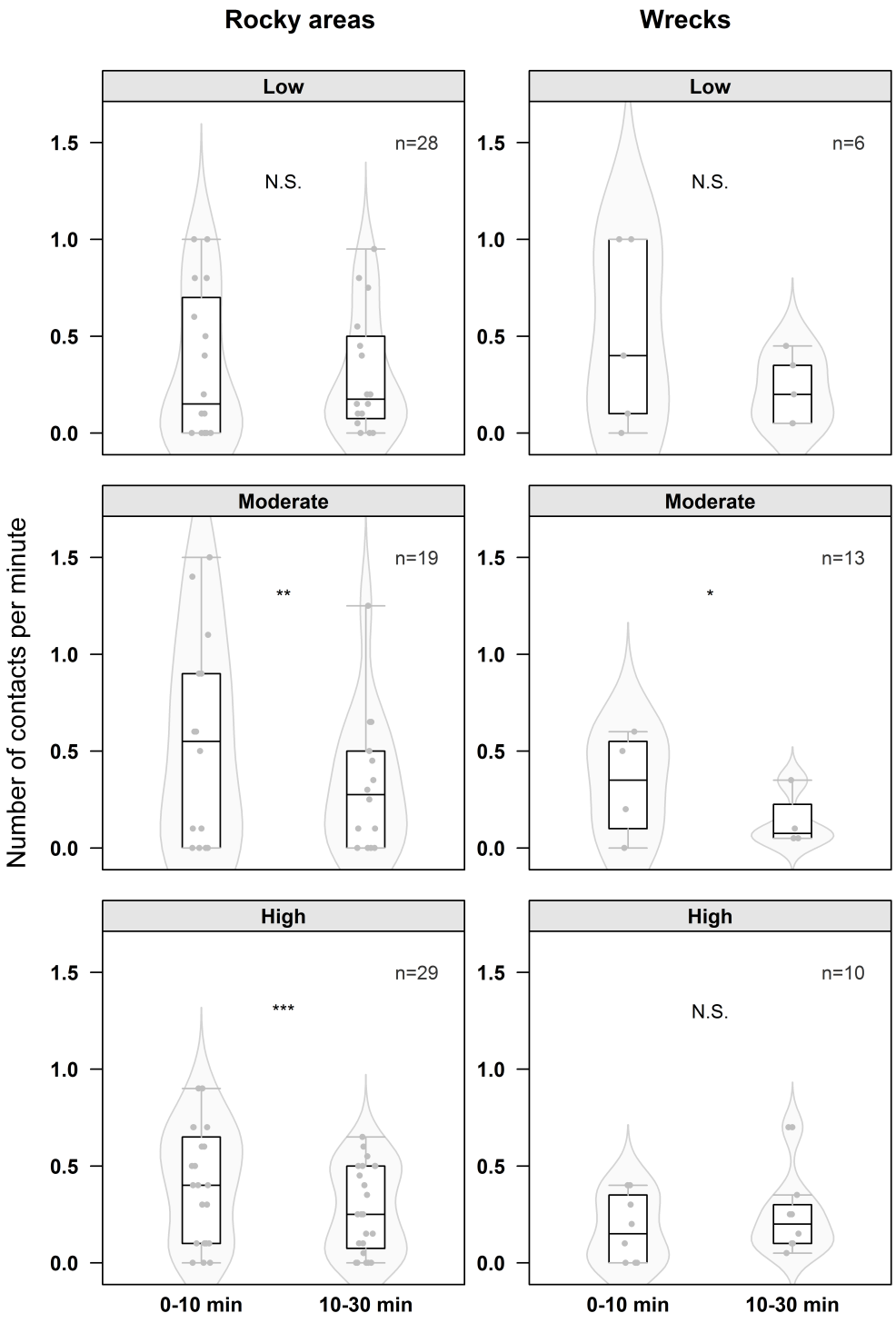

Figure 6.3.: Contact rates for rocky areas and wrecks discriminated by diving experience (low, moderate and high). n - number of samples; Friedman test used to compare the initial 10 min and the 10–30 min of the dive. N.S. - non-significant, * - $p < 0.05$, ** - $p < 0.01$ and *** - $p < 0.001$.

Contact rates (total dive, 0–10 min and 10–30 min) generally decreased with increasing experience of the diver (Table 6.1). However, only the difference in the contact rates of the initial part of the dive (0–10 min) of moderate and high experience levels of wreck divers were found to be significant (Wilcoxon test, $z = -0.72$, $p < 0.01$). Contact rates in rocky areas were generally higher than in wrecks, but no significant differences were found when comparing the two types of dive sites (Wilcoxon test, $p > 0.05$).

6.3.4. Impacts on marine ecosystem

The vast majority of "contacts" that were observed during the surveys were physical contacts with the substrate and marine organisms (mostly unintentional) and only a few cases of interactions with biota (97.1 % vs. 2.9 %). In rocky areas, 52.5 % of the contacts were fins touching the substrate or organisms, 23.0 % were hand contacts, 14.3 % were body contacts (Figure 6.4) and 7.4 % were gear contacts. Interactions with fauna were rare (2.7 %). A different pattern was observed in wreck areas mainly because contacts were made primarily using hands (48.6 %), followed by fins (22.4 %) whereas gear, body and interactions with fauna presented similar percentages to those observed in rocky areas (Figure 6.4).

Both at rocky areas and wrecks, it was impossible to discern any immediate consequence of a large quantity of the contacts (Unidentified, 58.4 % and 73.3 %, respectively). On the other hand, some of the contacts had a clear consequence. The most frequent case at both dive site types was the re-suspension of sediment (raising sediment, 29.0 % and 14.8 %, respectively), whereas the remaining actions and their consequences directly involved the biota living at the seafloor. In rocky areas, a total of 103 contacts with marine species were made and had different consequences, namely the disturbance of fauna (mainly fish, cephalopods and crustaceans; 4.5 %), contacts with colonial invertebrates without breakage (contact with fauna, 3.5 %), contacts with macroalgae (contact with flora, 3.1 %), breaking of colonial benthic species (gorgonians and bryozoans, 1.3 %) and a single event of fish feeding.

Regarding the possible effects of the contacts on the habitat as a whole, both at rocky areas and wrecks, most were rated by the observers as low (74.2 % and 86.7 %, respectively) and a total of 21 contacts were considered as having a high potential to harm the marine environment with similar percentages at both dive site types. The relative percentage of contacts presenting moderate impact was two times higher for rocky areas than for wreck areas (23.7 % and 11.4 %, respectively). Actions rated as low impact were the contacts with macroalgae and sediment re-suspension (88.0 % and 68.6 %, respectively) as most of the contacts which were classified as undetermined due to observation constraints (Unidentified; 84.5 %). On the other hand, organism breakage, disturbance and contacts with fauna were primarily associated to moderate and/or high

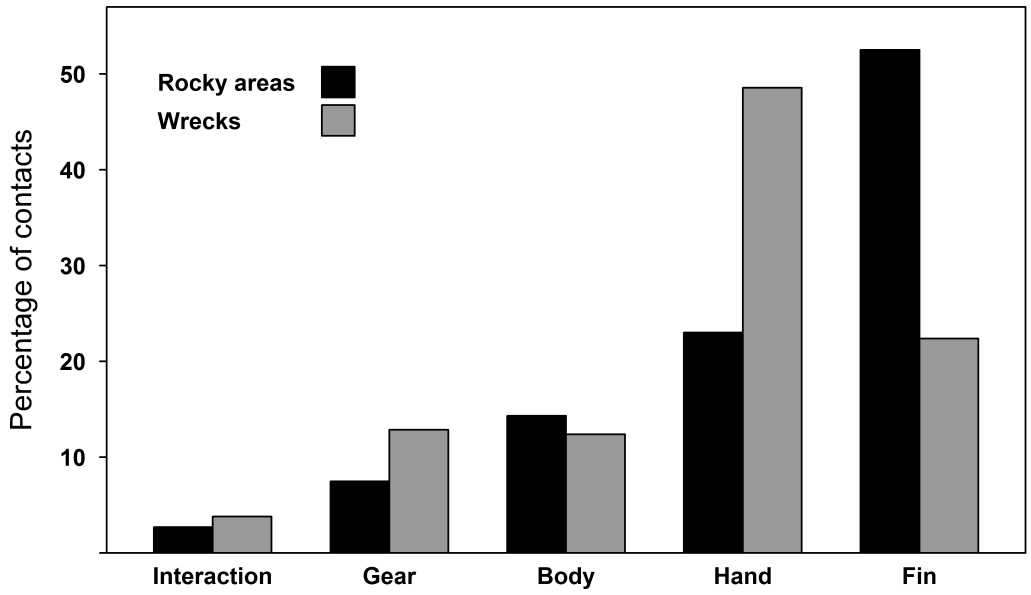

Figure 6.4.: Comparison of the relative distribution of actions in the two types diving sites.

impacts (63.6 %, 52.7 % and 47.2 %, respectively; Figure 6.5). Moderate/high impact events were more frequent in rocky areas, such as organism breakage (not observed at wrecks) and fauna disturbance were more frequent in rocky areas (Figure 6.5). The latter consisted mainly on scuba divers harassing the marine fauna, namely chasing fish and cephalopods, distressing octopus or cryptic fish species in their hides and holding echinoderms or other invertebrates.

6.4. Discussion

Diving has been frequently associated to habitat degradation, with higher damage levels in dived sites than in nearby non visited sites (Hawkins et al., 1999; Tratalos and Austin, 2001; Hasler and Ott, 2008). In coral reef areas, the coral cover decreased in sites intensively dived (Tratalos and Austin, 2001; Hasler and Ott, 2008) and damage especially of massive and branching corals is high (Hawkins et al., 1999; Zakai and Chadwick-Furman, 2002; Hasler and Ott, 2008; Leujak and Ormond, 2008).

Most impacts result from direct contacts with the fins to the substrate and marine fauna (Rouphael and Inglis, 1997, 2001; Zakai and Chadwick-Furman, 2002; Barker and Roberts, 2004; Uyarra and Coté, 2007; Leujak and Ormond, 2008), which was confirmed in the present study. Contacts with hands were also frequently observed, as it has also been reported elsewhere,

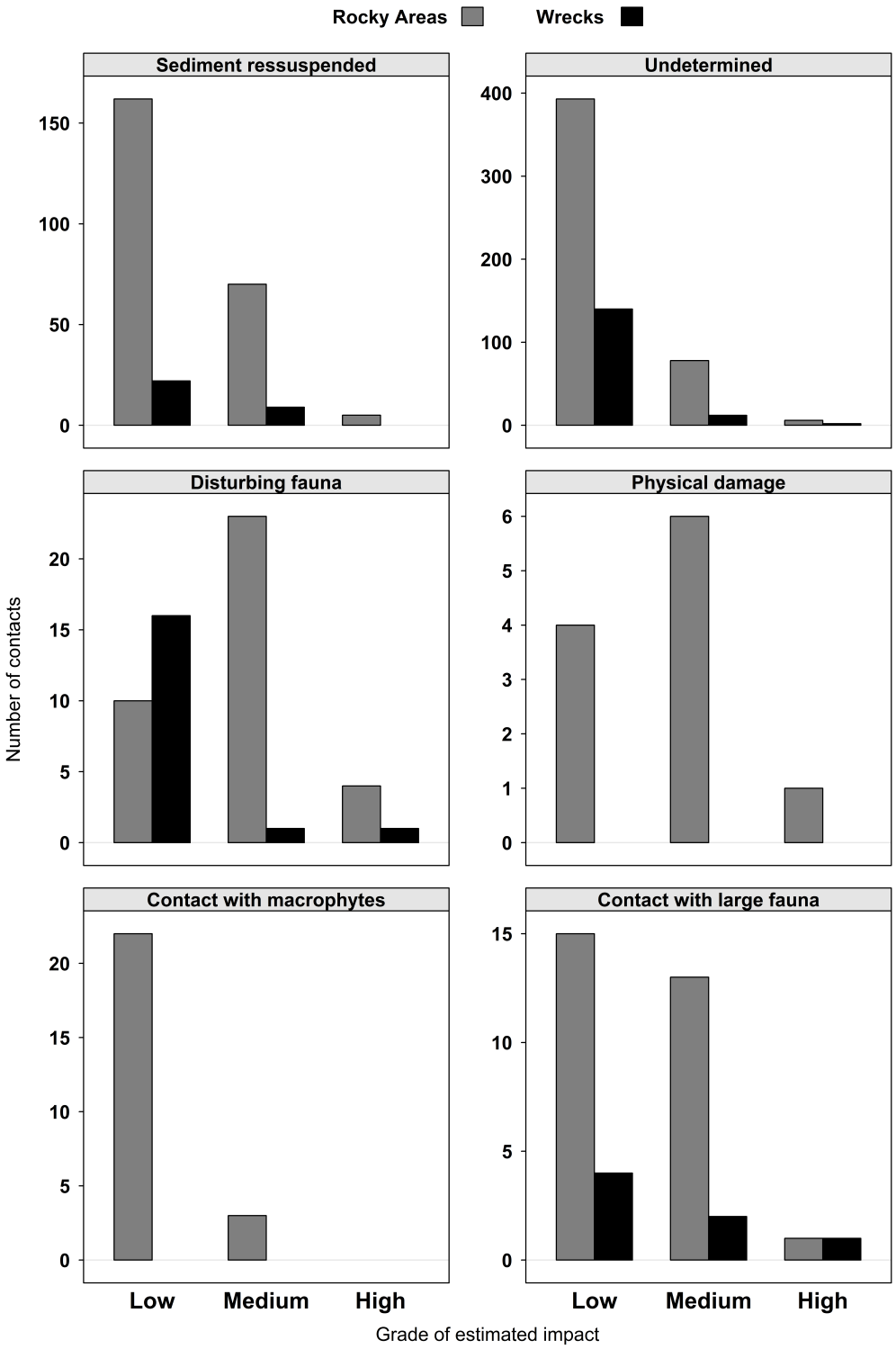

Figure 6.5.: Main consequences of the contacts of scuba divers. Number of contacts are presented for rocky areas and wrecks, discriminating impact grades (low, medium and high).

especially in coral reefs (Rouphael and Inglis, 1997; Zakai and Chadwick-Furman, 2002; Barker and Roberts, 2004; Uyarra and Coté, 2007; Leujak and Ormond, 2008; Luna et al., 2009). Hand contacts dominated in wreck areas, most of them intentional contacts conducted by moderate experience divers, probably because these scuba divers actively search for objects and fauna (entrances, holes). Active search for some animals, especially cryptic species, has been found to dramatically increase the rate of contacts and the damage inflicted to the benthic environment (Uyarra and Coté, 2007). Nevertheless, in the present study, intentional contacts to interact with fauna accounted for less than 5 % at both rocky areas and wrecks.

The main impacts on the environment (mainly on local fauna) resulting from contacts with the fins were the re-suspension of sediment and the subsequent persistence of nepheloid layers, as well as the physical contacts with fauna (with different outcomes, e.g. breakage, tissue abrasion). Indeed, occurrence of nepheloid layers may lead fish and motile invertebrates to avoid the area and affect suspension-feeding sessile organisms such as gorgonians (Sala et al., 1996; Garrabou et al., 1998; Milazzo et al., 2002; Zakai and Chadwick-Furman, 2002; Airoldi, 2003; Balata et al., 2005; Leujak and Ormond, 2008; Luna-Pérez et al., 2011) and ascidians (Luna-Pérez et al., 2010, 2011). Direct contacts to the fauna may damage important habitat building species, such as stony corals, gorgonians, sponges and bryozoans, significantly contributing to habitat deterioration (Sala et al., 1996; Garrabou et al., 1998; Hawkins et al., 1999; Coma et al., 2004; Uyarra and Coté, 2007; Hasler and Ott, 2008; Leujak and Ormond, 2008; Di Franco et al., 2009). In this study, we observed scuba divers unintentionally breaking, sometimes extensively, large bryozoans such as *Pentapora fascialis*. These fragile colonial organisms are frequently damaged in intensively used dive sites resulting in important effects in density, size and coverage, altering the structure of this species' populations (Sala et al., 1996; Garrabou et al., 1998). Although this species is known to recover rapidly from disturbance (Coma et al., 2004) it has potential as an indicator for scuba diving impacts.

The most conspicuous fauna in dived areas of the Algarve is, however, a mixed assemblage of gorgonian species, especially *Eunicella labiata*, *Eunicella gazella*, *Eunicella verrucosa*, *Leptogorgia lusitanica* and *Leptogorgia sarmentosa* (Cúrdia et al., sub.a). Although not very frequent, trampling over gorgonians was observed in the present study, with consequent damage to gorgonian tissues and leading to partial mortality and breakage. Partial mortality in gorgonians results in reduced growth and reproductive effort and to a higher risk of predation and colonization by epifauna (Coma et al., 2004; Linares et al., 2008c). In the Algarve, gorgonians are among the largest benthic animals, providing habitat for other species and enhancing local biodiversity (Carvalho et al., sub.). These long-lived animals have typically low recruitment rates, low growth and long turnover-times (Mistri and Ceccherelli, 1994; Coma et al., 1998a, 2004; Linares et al., 2008b). Consequently, damage produced by diver contact becomes a more severe and chronic disturbance due to low recoverability (Coma et al., 2004; Di Franco et al., 2009; Luna-Pérez et al., 2010).

Interactions with fauna (chasing fish, playing with seastars, octopus and cuttlefish) may also result in moderate to high impacts on local fauna, as stress resulting from the interactions may increase the probability of animals being predated, cause energy waste and disrupt crucial phases of species' biological cycles (Frid and Dill, 2002; MacFarlane and King, 2002; Chuchman, 2006; Cubero-Pardo et al., 2011; Teresa et al., 2011), namely spawning (Heyman et al., 2010). Furthermore, some species (e.g. groupers) are more sensitive than others (e.g. snappers) and daily visits by scuba divers of a "permanent" spawning aggregation site can create sufficient disturbance for fish species to move to other areas (Heyman et al., 2010). Another common interaction with fauna (yet rarely observed in this study) is fish feeding which has been proved to affect directly and indirectly the structure of coastal fish assemblages (Milazzo et al., 2005, 2006; Ilarri et al., 2008). The extremely low frequency of fish feeding in the present study probably resulted from a general awareness of the diving centres that systematically advise divers on the detrimental effects of fish feeding.

Even though scuba diving is a rather small industry in the Algarve, its growth in the past few years and the national and regional strategy to maintain tourism as an important source of income for the region (Anonymous, 2006; Correia and Pires, 2006), suggests that the pressure on the marine ecosystem posed by this recreational activity may increase rapidly. Moreover, considering that 15 % of the divers do moderate/high impact contacts with rates above 1.5 contacts 10 min^{-1} the threats to marine habitats will increase.

The main conclusions of the present study are:

1. experienced divers present lower contact rates than moderate and low experienced divers (specialization matters)

2. contact rates are highest in the initial part of the dive (time matters)

3. contact rates in wrecks are lower than in natural rocky areas and

4. most contacts in natural rocky areas are fin contacts whereas in wrecks hand contacts dominate (dive site types present different diving profiles)

Facing these main findings, some measures can be applied in order to prevent and/or reduce the damage inflicted to marine communities. As increased knowledge and skills (specialization) are determinant for changing the behaviour of scuba divers, improved diver training is a key factor to minimise their negative impacts on the seafloor (Thapa et al., 2005, 2006; Ong and Musa, 2011). Specialization should be reinforced by educational programs that can be formulated by various stakeholders (e.g. marine conservation organizations, governmental agencies and the diving industry) (Thapa et al., 2006; Pepe, 2010; Ong and Musa, 2011). Environmental

awareness influences the scuba divers' behaviour (Ong and Musa, 2011), therefore educational and certification programmes should include elements on general marine conservation issues and on the environmental impact of diving (e.g. videos of scuba divers' actions and their consequences) which may eventually build a responsible diving behaviour (Rouphael and Inglis, 1997; Zakai and Chadwick-Furman, 2002; Thapa et al., 2006; Dearden et al., 2007; Pepe, 2010; Ong and Musa, 2011). These programs should emphasize positive actions to preserve the marine ecosystem advising on good-practise and code of conduct during dives and promoting continued education and "eco-friendly" social activities (Thapa et al., 2006; Ong and Musa, 2011), instead of focusing on penalties, boundaries and prohibited activities (Ong and Musa, 2011). Pre- and post-dive briefing sessions, conducted by a divemaster have been strongly recommended (Rouphael and Inglis, 1997; Schleyer and Tomalin, 2000; Thapa et al., 2006; Dearden et al., 2007; Ong and Musa, 2011) and proven to be successful at reducing impacts (Medio et al., 1997; Barker and Roberts, 2004; Uyarra and Coté, 2007). But the content of the session should extend beyond rules, regulations and safety procedures, providing information about diving sites, particular features of the aquatic environment (including marine life), diving conditions or needed diving skills needed (Ong and Musa, 2011). Experienced scuba divers tend to erroneously perceive that the amount of damage they may cause is relatively minor and, therefore, are less likely to modify their own behaviour (Rouphael and Inglis, 2001). In this regard, briefings are likely to be more effective if they emphasize the potential for cumulative impacts as a result of the sum of relatively minor effects of many individual divers and/or successive dives (Rouphael and Inglis, 2001). A diving code of conduct can be integrated by dive masters and instructors into pre-dive briefings and other diving courses which may help to reinforce the importance of ethics and responsible behaviour (Thapa et al., 2006). It is important to emphasize that the training of divemasters and instructors is also fundamental to achieve this goal. The intervention of divemasters to alert and correct unintentional/intentional behaviours proved to be significant at reducing the number of contacts, and therefore at reducing the scuba diving impacts on marine habitats (Medio et al., 1997; Luna et al., 2009). Therefore, as suggested elsewhere, all dives should be guided by trained divemasters or dive guides (Zakai and Chadwick-Furman, 2002; Barker and Roberts, 2004; Luna et al., 2009). Their example in keeping hands and equipment away from the substrate and vigilance especially at the beginning of dives and towards the users of special equipment (cameras, flash-lights) or dives (night dives), may significantly reduce the impacts (Barker and Roberts, 2004). Small groups are advisable as this will ease the ability of dive leaders to perform their supervisory role (Rudd and Tupper, 2002; Barker and Roberts, 2004).

Taking into account that impacts were higher at the initial part of the dive and in natural rocky areas than in wrecks, carefully planning of scuba diving trails and starting the dive in areas with lower benthic cover are good measures to reduce the number of contacts. Locating training courses and introductory dives in sandy areas or nearby artificial reefs is also advisable as, whenever possible, recreational diver pressure must be diverted away from natural coral reefs

to artificial reef areas (Zakai and Chadwick-Furman, 2002; Hasler and Ott, 2008). In the Algarve, scuba divers prefer to dive in preserved natural reefs looking to observe unusual fish or other less common aquatic organism, but they also state a high preference for wrecks, namely those with archaeological interest and sunken vessels (Ramos et al., 2006). In addition, the data presented here suggests that in wrecks, contact rates are generally lower, globally reducing the impacts of scuba diving. However, due to the relatively low number of samples (29) data should be addressed with caution. Ships have been sunk worldwide to enhance the scuba diving market at the local level (Abelson, 2006; Seaman, 2007) and their economic value has already been documented (Morgan and Massey, 2009, and references therein). However, the medium/long term effects of sinking decommissioned vessels are poorly studied. Despite the preparation that is usually involved in the process, degradation of vessel materials and leakage may increase concentrations of hazard materials and result in contamination, and other possible negative impacts such as community structure shifts in fish and macrobenthic assemblages (attraction of fish species) and spread of invasive species (Johnston et al., 2003, 2005; Davis et al., 2007; Glasby et al., 2007). Therefore, sinking vessels for scuba diving must be carefully planned to predict environmental hazards and when implemented, long-term monitoring using multidisciplinary approaches is strongly recommended.

It is important to integrate legal, scientific and management tools in order to build robust conservation plans. In more sensitive areas, diving can be restricted to experienced divers and/or diving quotas may be applied to reduce impacts (Luna et al., 2009). Research should be carried out to investigate the benthic community vulnerability and resilience and assess sensitivity to diving impacts (Lloret et al., 2006). Also, monitoring programmes (Milazzo et al., 2002) using vulnerable or sensitive species (e.g. gorgonians and bryozoans) as focal species should be implemented to assess the success of management measures (Garrabou et al., 1998; Coma et al., 2004; Di Franco et al., 2009; Luna-Pérez et al., 2010, 2011).

The estimated number of 5390 divers using scuba diving centres in the area (for the year 2004, Santos et al., 2006) is much lower than the estimated 11 200 divers yr^{-1} of the Parque Marinho Luís Saldanha, the most important diving location in Portugal (Rodrigues, 2008) and also lower than the mean 7123 divers yr^{-1} of European MPAs (Roncin et al., 2008), and may be lower than the carrying capacity of the system. The Algarve coast yields attractive habitats of high biodiversity and ecological importance, harbouring vulnerable benthic fauna and it is subjected to multiple purposes. The main results of this study suggest that these focal points should be addressed with caution and used to define the guidelines for carrying capacity estimation in the region. As pointed out by Luna et al. (2009, see references therein) scuba diving carrying capacity vary extensively between different sites/areas around the world, due to several factors, such as physical conditions, natural disturbance events, biological communities in the area and anthropogenic pressures. As a consequence, the real carrying capacity of the system is dynamic and any measure to be used for

management purposes should be adapted to each particular dive site and reviewed periodically (Luna et al., 2009).

Acknowledgements

J.C. (SFRH/BD/29491/2006) benefits from a PhD grant from the “Fundação para a Ciência e a Tecnologia” (FCT)’. This study was supported by INTEREG IIIB - MEDOCC under the project “SUBMED - Strategy for the sustainable development of underwater tourism in the Mediterranean”. The authors would like to thank to the diving centres “Hidroespaço”, “Torpedo” and “Divetime International” for the help during dives and information to characterize the scuba diving activity in the Algarve.

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Conclusions

C.1. Conclusions

Ecological relevance of gorgonian gardens

Shallow water gorgonian assemblages in Southern Portugal are mainly characterized by a co-dominance of several species (*Eunicella labiata*, *Eunicella gazella*, *Eunicella verrucosa*, *Leptogorgia lusitanica* and *Leptogorgia sarmentosa*) that do not compete themselves for space but, because of different habitat requirements or preferences, occupy different niches. *Leptogorgia sarmentosa*, for example, is mainly found in areas where the re-suspension of sediments is common, whereas *Leptogorgia lusitanica* is frequently observed in places with stronger currents (vertical walls) and open spaces with low sedimentation (terraces).

The abundance of gorgonians increases with depth showing a negative correlation with erect algae. The abundance of algae generally decreases with depth because light is a limiting factor, and the benthic cover becomes dominated by animals probably due to lower competition for space with algae. On the other hand, a positive correlation between the abundance of gorgonians and the abundance of sponges (Porifera) was observed. Because of their quasi bi-dimensional erect shape, gorgonians do not occupy a large space in the substratum, which may be used by other benthic groups such as sponges, bryozoans, other cnidarians or coralline algae, maximizing space occupancy, heterogeneity and complexity of the sea-bottoms, and ultimately biodiversity.

Colonies of *Eunicella gazella* and *Leptogorgia lusitanica* in the studied sites presented a diverse (11 phyla, 181 taxa) and abundant (7284 individuals) associated fauna, numerically dominated by amphipods but with polychaetes contributing the most to diversity. The analysis of diversity patterns, within and between gorgonian hosts, at both spatial and temporal scales, showed that these two gorgonians were somehow complementary to the biodiversity of the habitat as a whole. Gorgonian host, colony size and time were the most important factors in determining high levels of diversity. The results suggest that biodiversity patterns are better defined by differences in relative abundances rather than in species composition. Even though the ecological function of both species is not entirely redundant, each adding new niches to the system and supporting attendant assemblages, the two gorgonians (all colonies pooled) shared most of the species collected, and only 11 and 18 mostly rare or uncommon taxa were exclusively associated with *Eunicella gazella* and *Leptogorgia lusitanica*, respectively (excluding singletons). The abundant unidentified white flatworms (Turbellaria) in *Eunicella gazella* colonies was the only exclusive species to show a significant association to its host which may be explained by crypsis with the white colour of the gorgonian branches.

The differences in attendant assemblages, were partially explained by species-specific attrib-

utes (size, complexity, lacunarity) but the main structuring factor appears to be the presence and fouling level of colonial epibionts (e.g. hydrozoans, sponges) and algae. Possibly due to a trophic effect (direct or indirect enhancement of food availability) combined with surface availability for colonization (species-area effect), "colonial epibiont cover" was the strongest predictor of species richness and abundance of gorgonians' attendant assemblages. Moreover, the validity of the paradigm that structural complexity enhances biodiversity may be scale-dependent and, in the case of gorgonians, the effect of complexity at the "garden" level may be much more relevant than at the individual colony level. These findings reinforce the need for the conservation of gorgonian aggregation areas as a whole in order to preserve host diversity and size structure.

Life history

Shifts, resulting from disturbance or protection, may lead to different effects in species with different traits (Halpern and Warner, 2002; Claudet et al., 2010), therefore the knowledge on the life history and traits of species, especially those more vulnerable to impacts is extremely important for marine conservation. Longevity, time to maturity, reproductive mode, fecundity and propagule dispersal are some examples of traits conditioning the distribution patterns and the population dynamics of marine benthic species (Bremner, 2008), especially because of the importance of the earliest life history stage (egg or larva in gorgonians) (e.g. Linares et al., 2007, 2008b; Cowen and Sponaugle, 2009).

The oogenic cycle of *Eunicella gazella* is long (over one year), with colonies presenting high fertility and spawning of mature oocytes occurring in September/October. The spermatogenic cycle occurs over a shorter period of time (eight to ten months), but maturation and spawning of both sexes is highly synchronized. Temperature seems to govern the maturation of gonads, probably being related both to metabolic efficiency and food availability. Broadcast spawning is preliminarily pointed out as the mode of reproduction but more studies are needed in order to fully understand this reproductive feature. However, the study on the gametogenesis of *Eunicella gazella* does shed light on the reproductive pattern of one of the most abundant and common gorgonian species of the Algarve, but for which no data was available on any reproductive aspect. Even though the present study could not find a clear effect of colony size on fertility, further studies should be specifically designed to ascertain this issue. The gametogenic cycle of other species that are frequent and abundant should also be studied, especially for *Eunicella labiata* and *Leptogorgia lusitanica*, as reproductive data on these species is entirely missing. On the other hand, *Leptogorgia sarmentosa* and *Eunicella verrucosa*, should also be studied as the information available to the moment is still scarce (a single study for each species).

Impacts

Despite the high biodiversity associated with gorgonians, they are subjected to several pressures. The present study presents evidence that the population structure of gorgonian assemblages along the southern coast of the Algarve, can be related not only to differences in the physical characteristics of each area but also to the natural and anthropogenic pressures that act specifically upon them. In the case of anthropogenic pressures, fishing is pointed as the most probable damaging factor, as all the remaining activities do not seem to have broad regional differences. In disturbed areas (due to fishing and/or frequent sedimentation) gorgonian populations were dominated by small-sized colonies, clearly different from the population structure of areas under lower disturbance. Because several biological processes are density-dependent or size-dependent (e.g. Kapela and Lasker, 1999; Vermeij and Sandin, 2008; Tanner et al., 2009; Forrester et al., 2010), this information is of utmost importance for the study of those processes. On the other hand, damage in gorgonian colonies in fishing areas was commonly observed (broken colonies; entangled nets, angling lines and cables from cages; recently detached colonies with different damage levels implying frequent disturbance) and sometimes extensive. Indeed, preliminary results concerning damage assessment in gorgonian colonies along the Algarve southern coastal waters further support the assumption that fishing may exert a high pressure on gorgonian assemblages. In two natural reef areas with high fishing intensity, Pedra da Greta and Pedra do Barril, colony damage (fouling, denuded axis, breakage; estimated underwater) was assessed in gorgonian colonies of *Leptogorgia lusitanica*, *Leptogorgia sarmentosa*, *Eunicella gazella* and *Eunicella labiata*. It was found that the percentage of damaged colonies was high at both sites and all species, ranging from 81.3 to 100 %. However, some differences were found between the two genera, with *Leptogorgia* species being mainly characterized by small damaged colony areas, whereas *Eunicella* colonies were extensively damaged (see Figure C.1). The *Leptogorgia* were mainly damaged in the tips of the colonies, probably due to abrasion with seafloor or other biota as they are very flexible, presenting low percentage of broken colonies, 5.5–9.6 % and 18.8–25.0 % for Pedra da Greta and Pedra do Barril, respectively. This kind of colony structure copes well with trampling from fishing traps, for example, because as soon as the gear is hauled the colony reverts to its upright position. On the other hand, *Eunicella* colonies presented extensive fouling by algae (mainly in the tips), bryozoans, barnacles and anemones and were frequently entangled in fishing gears. Furthermore, a large proportion of the sampled colonies were broken (12.9–50.0 %), especially *Eunicella labiata* that showed 43.3 and 50.0 % of broken colonies in Pedra do Barril and Pedra da Greta, respectively. Contrastingly, underwater observations in areas under lower fishing intensity suggested that gorgonians present much lower damage rates and the extension of lesions is also much lower.

For several decades tourism has been increasing in the Algarve region and scuba diving is

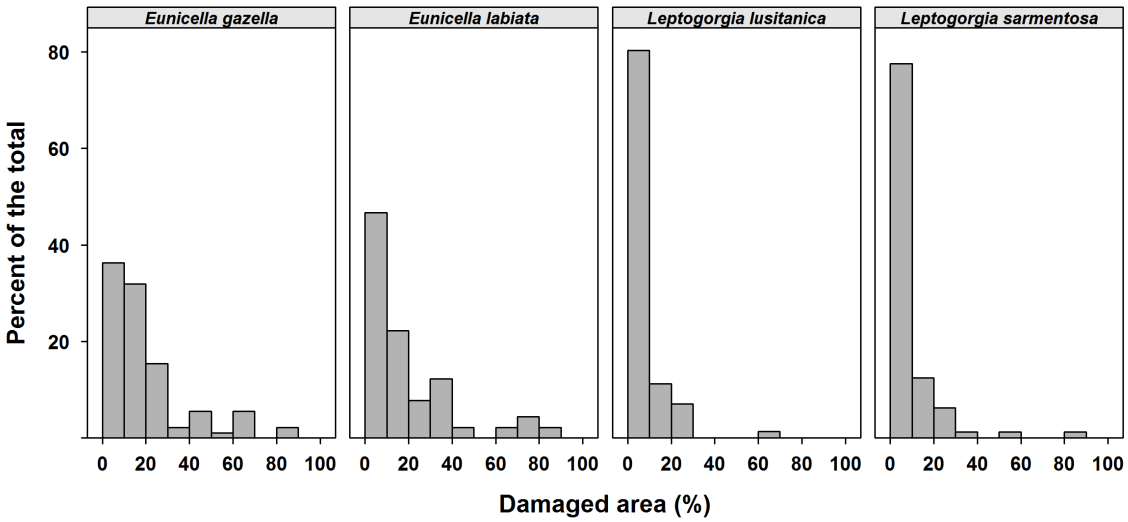

Figure C.1.: Histogram of the percentage of damaged colony area for *Eunicella gazella*, *Eunicella labiata*, *Leptogorgia lusitanica* and *Leptogorgia sarmentosa*.

one of the recreational activities which promotes a particularly direct interaction with gorgonian gardens. However, at least regarding scuba diving, at present levels, this activity does not seem to compromise gorgonian assemblages. The present study indicates that scuba divers in the Algarve make contacts to the seafloor and benthic biota, impacting marine rocky habitats, especially in the initial part of the dive. Even though the impacts are generally low, the increasing trend of the activity in the region may lead to greater impacts. What is more, some of the impacts present high damage, such as breakage of sessile benthic organisms. This is particularly important when the affected organisms are ecologically important (habitat formers) but characterized by low recruitment rates, low growth, long lifespan and long turnover-times, such as gorgonians. In these cases, regeneration may impair for example growth and reproduction, leading to more severe and chronic disturbance effects due to low recoverability.

C.2. Final remarks

The joint effect of small-sized dominated colonies in disturbed areas and the fact that the enhancement of biodiversity promoted by gorgonians is size-dependent, the reduction of gorgonian populations and the shift towards smaller sizes due to fisheries impacts will implicate a decrease in the local biodiversity (α and β diversity) with possible implications for the shallow rocky subtidal (meta)community. The lower population size, smaller colonies and damaged colonies may also decrease the ecological services attributed to gorgonians (e.g. scuba diving, fish

protection). Most sessile marine organisms depend on water circulation to promote the encounter of gametes. In many corals, one of the species traits to increase reproduction success is sperm concentration and high synchronization of spawning, leading to huge mass spawns, sometimes of multiple species (e.g. Babcock et al., 1986; Harrison, 2011). If population size drops below a certain threshold, the concentration of gametes may be insufficient to guarantee the normal rates of fecundation of oocytes leading to reproductive failure, thus reducing population growth rates, sometimes to negative values, increasing the risk of extinction, a classic example of an Allee effect (Courchamp et al., 1999; Stephens and Sutherland, 1999). There is growing evidence that these negative density dependent effects are important for species conservation efforts and fisheries management (Stephens and Sutherland, 1999; Gascoigne and Lipcius, 2004; Courchamp et al., 2008).

For most marine species, but especially for sessile benthic species, the pelagic larval phase represents the primary opportunity for dispersal (Cowen et al., 2006; Cowen and Sponaugle, 2009) as long as they produce more larvae than the necessary to assure self-recruitment (source population). Marine populations suffering continuous impacts rely on larval import from nearby areas to face extinction and to balance the local negative population growth (Cowen et al., 2006; Krebs, 2008; Cowen and Sponaugle, 2009). Therefore, the persistence of metapopulations relies greatly in the larval dispersal capacity between populations (connectivity). The connectivity between marine populations is very complex, depending on local oceanographic conditions (spatially complex), stochasticity (yearly fluctuations, natural disturbance) and biological traits (vertical movements, interactions), which differ greatly between species (Cowen et al., 2007; Jones et al., 2007; Cowen and Sponaugle, 2009). Furthermore, in the last decade several studies pointed that dispersal can be much lower than previously expected (see Cowen et al., 2000, 2007; Cowen and Sponaugle, 2009; Jones et al., 2009), and therefore connectivity has the potential to strongly influence local populations (or metapopulations) with consequences for the structure, dynamics and biodiversity of communities (or metacommunities).

Implications, applications and recommendations

Under the current scenario of multiple uses, impacts and climate change on spatially complex and dynamic systems, such as coastal areas, density dependent effects, connectivity between metapopulations and biotic interactions all play important roles in the sustainable use of those ecosystems. Marine Protected Areas (MPAs), or marine reserves if they encompass a “no take” zone, have been largely used as management tools with two main objectives, fisheries management and biodiversity protection (e.g. Pauly et al., 2002; Lubchenco et al., 2003; Jones et al., 2007; Lester and Halpern, 2008; Pérez-Ruzafa et al., 2008). The conservation of marine ecosystems in Portugal is mainly regulated by European directives that were transposed to national laws,

and to international conventions that were signed and ratified by Portugal (Birds and Habitats directives, Natura 2000). The European Union, encourages its members to reach the goal of creating at least 10 % of Marine Protected Areas (MPAs) by 2020 (Aichi Biodiversity Target 11, http://www.cbd.int/sp/targets/). OSPAR, also points to the development of a network of Marine Protected Areas as to protect biodiversity and ecosystem functioning in the North-East Atlantic. However, to the author best knowledge, there is currently any plan to achieve such percentage of MPAs in Portugal mainland in the near future.

Recently, Lester and Halpern (2008) proved that reserve effects are higher in no-take reserves than in partially protected areas, namely regarding biomass, density, species richness and organism size. These management tools have been successful in preventing coral loss besides other advantages and benefits (e.g. Selig and Bruno, 2010; Graham et al., 2011). Location and size of MPAs greatly determine their outcomes, because coherent sets of marine reserves should encompass a representative area and collectively represent all the components of the regional biodiversity. Also, MPAs should have a spillover effect replenishing populations of the adjacent non protected areas, but in order to fulfil this requirement, metapopulation dynamics must be ensured through connectivity. This is the reason why currently networks of marine reserves are advocated. In fact, an efficient network of MPAs must include as many as possible distinctive habitats and several replicates of representative habitats, have individually or collectively the necessary size to support minimum viable populations of large species, but also to be oceanographically connected in a way that ensures an efficient recruitment amongst individual MPAs. These characteristics should foster the necessary resilience to a number of threats. The location of source populations (to be protected) is decisive for the connectivity at the local and regional level and will determine if a network of marine reserves is effective or not (Jones et al., 2007; Cowen and Sponaugle, 2009; White et al., 2010).

Overall, the results presented in this thesis highlight the ecological importance of gorgonians in the southern Algarve coastal waters, namely by the enhancement of biodiversity. Impacts on gorgonian assemblages and their distribution, abundance and structure patterns should be taken into account while planning local MPAs networks. The reproductive cycle of *Eunicella gazella* provides information that can trigger new studies with more ambitious objectives, such as the connectivity of benthic broadcast spawners and the species traits that can influence the processes involved. The information on scuba diving impacts can be used to manage this activity in the region and should also be taken into account in the design of MPAs, as scuba diving will probably be one of the uses on those areas. The impacts pointed out by this study can increase the awareness of scuba divers to adopt measures that may significantly decrease their impacts in the habitat. For example, gorgonians and other benthic species are proposed to be used as indicators of scuba diving effects, which can be transposed to management plans. Finally, the indication that gorgonians are frequently and extensively damaged and the difficulties

encountered in preliminary transplantation experiments, strongly emphasize the need for more short term studies focusing on the effects associated to colony damage and that conservation of gorgonian gardens is of high priority. These preliminary data need to be confirmed by further sampling and replicated in areas with different intensity of fishing pressure. Studies should also be conducted to analyse energy use in damaged and healthy colonies of all gorgonian species. According to the distribution and abundance data (part I) and the extension of damaged colony area, *Eunicella labiata* and *Eunicella gazella* should be focused primarily. This is one clear example of the usefulness of the information contained in this thesis in terms of future research but also for management purposes, suggesting also that more research is required to increase the probability of success of management plans.

Future research

The ecological importance of coral gardens is being acknowledged, as a consequence of studies concerning the ecology and biology of these habitats. Because this is the first contribution on the ecology and biology of gorgonians for Southern Portugal and the second for the country, many aspects were not addressed at all and much work still needs to be done. However, it is expected that the information of this thesis, contributing for the knowledge of gorgonian populations, shall be used for management and future research.

Although in the Algarve coastal waters, fisheries have been thoroughly studied regarding landings, fishing yield, by-catch and selectivity, mapping of the fishing intensity is not available. Therefore, it was extremely difficult to predict the fishing pressure of each area. The observation of lost fishing gears in a certain area, their quantity, diversity and degree of degradation; the number of fishing boats (professional and amateur) in a certain area along time; fishing gear tracks, provide indirect evidence of fishing intensity. However, these methods are extremely laborious, time consuming and expensive. The monitoring of fishing vessels in real time using advanced positioning systems (vessel tracking systems with GPS) would prove important to provide accurate and updated information to be used for quantifying fishing pressure dynamics. A database of lost fishing gears (date, coordinates, quantity, type) based on fishermen reports, and complemented by other sources such as scuba diving centres and governmental agencies, would also allow to further assess the threats to local populations. This data incorporated into GIS with multiple data sources (landings, vessel data, habitat mapping) would be able to provide maps of use and intensity that can be used for the management of the coast. This type of information is extremely important for MPAs planning and design, but also for ecological studies dealing with impact assessment, namely studies on damage assessment of gorgonians by fishing gears. It would also serve to discriminate the effects of natural disturbance from those of fishing activities both in abundance and size-frequency data.

On the other hand, climate change is probably one of the most challenging and important issues concerning marine ecosystems (e.g. Hoegh-Guldberg and Bruno, 2010). The effects of global warming go beyond physiological adaptation of species and consequent shifts in the structure of marine communities. Most certainly they will also result on changes in ocean and coastal circulation patterns possibly affecting the connectivity between habitats due to reduced dispersal of propagules. What is more, the chemical properties of sea water are changing, leading to ocean acidification which is a major threat to several species and even to entire ecosystems, such as coral reefs. Similarly to hard corals, many gorgonian species present calcium carbonate on the form of calcite with an important function on their form and structure. The calcification processes are changed by ocean acidification which may lead to changes in the physical properties of gorgonians affecting, if not their survival, at least their ecological role, ultimately reducing the biodiversity and resilience of habitats. In the last two decades, many benthic organisms, including gorgonians have suffered mass mortalities attributed to increased sea temperature and consequent disease outbreaks (e.g. Cerrano et al., 2000; Martin et al., 2002; Linares et al., 2005; Bally and Garrabou, 2007). Therefore, continuous monitoring of sea water temperatures with high spatial resolution (low cost temperature data loggers) would provide information on the spatial and temporal variability (and possible causes) which could be used to make predictable models to assess vulnerability of habitats, areas or species. Coastal water circulation models would be greatly improved with such data, especially if complemented by other methodologies (Conductivity, Temperature, and Depth, CTD sensors; Acoustic Doppler Current Profilers in areas of exceptional complexity) and additional data (e.g. coast and seafloor morphology). Robust coastal circulation models are extremely important for the implementation of MPA networks because connectivity is strongly influenced by water circulation.

At last, transplantation methods using small colony fragments are one of the measures that can be used in the future to restore the gorgonian populations affected by impacts (Rinkevich, 2000; Shafir et al., 2006; Shaish et al., 2008). During a first attempt to address this issue, preliminary results from transplantation experiments were not optimistic. Indeed, high mortality rates were observed probably due to a mix of important factors such as: high temperatures during the transplantation process as the experiment was conducted during the summer (August), and high sedimentation in the transplantation site. In fact, one month after transplantation, more than half of the transplanted fragments (42 transplants of 2 cm fragments of *Eunicella gazella*; 84 transplants of *Leptogorgia lusitanica* of two size classes, 2 and 5 cm, 42 each) were alive and apparently in good health (Figure C.2) even though some presented low levels of fouling by algae in the branch tips. However, three months after transplantation more than 85 % of the transplants died (Figure C.2). Some of the bases where the transplants were fixed were broken and the cables that hold them to the artificial reefs were cut, probably as a consequence of bad weather that displaced a set of ghost fishing traps that were found nearby. The remaining bases were completely covered with sediment and most of the transplants that were still alive presented partial damage and extensive fouling.

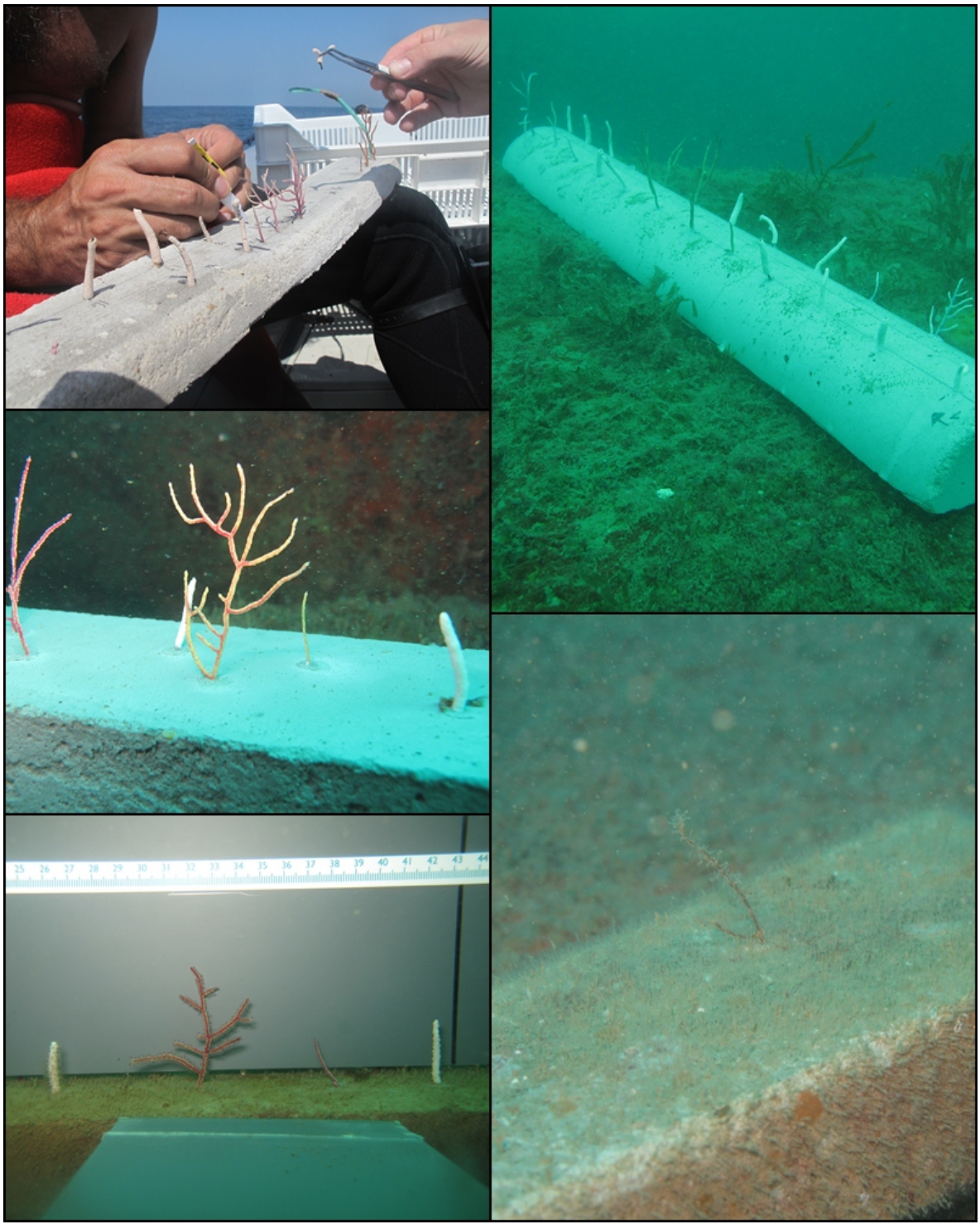

Figure C.2.: Transplanted fragments of *Leptogorgia lusitanica* and *Eunicella gazella*. **top-left:** transplantation of small fragments to cement bases; **top-right:** bases with transplants fixed to artificial reefs; **centre-left and bottom-left:** transplants one month after transplantation; **bottom-right:** dead transplant of *Leptogorgia lusitanica* on base completely covered with sediment. Photos by João Cúrdia and José Luís Sofia

These experiments could benefit from a better knowledge on the suitable conditions for achieving acceptable survival rates (e.g. temperature threshold). This kind of information can be obtained through controlled experiments in aquaria in relation to the physiology and biology of gorgonians. Some examples are the effects of increased temperature on growth, stress, reproductive output, metabolism and feeding of gorgonians. They are also important to gain knowledge on some aspects of the reproductive biology of gorgonians, such as spawning, fertilization and larval development, otherwise only possible through difficult, laborious and expensive in situ studies. All this information is missing for the most common and abundant gorgonian species of the Algarve. However, it is of utmost importance to understand the full life cycle of these benthic organisms. The results of such experiments can be used to build predictable models for future scenarios, as is being done for other octocoral species such as *Paramuricea clavata* (Linares et al., 2007, 2008d) and *Corallium rubrum* (Torrents et al., 2008). Furthermore, the use of gorgonians in restoration efforts and harvesting for the industry of natural products (if they cannot be synthesized), involves the sexual or asexual (vegetative) reproduction of gorgonians and their rearing to a suitable size for transplantation or harvest, which greatly depends on the information regarding the life cycle of the species.

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